Interactions between Atlantic cod *(Gadus morhua)* and capelin *(Mallotus villosus)* off Labrador and eastern Newfoundland: a review

G.R. Lilly

Science Branch
Department of Fisheries and Oceans
P.O. Box 5667
St. John's, Newfoundland A1C 5X1

September 1987

Canadian Technical Report of Fisheries and Aquatic Sciences No. 1567

Fisheries and Oceans Pêches et Océans

Canada

88-01576/

Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of the Department of Fisheries and Oceans, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in *Aquatic Sciences and Fisheries Abstracts* and indexed in the Department's annual index to scientific and technical publications.

Numbers 1–456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457–714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715–924 were issued as Department of Fisheries and the Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page. Out-of-stock reports will be supplied for a fee by commercial agents.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. Il n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques du ministère des Pêches et des Océans, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications complètes. Le titre exact paraît au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la revue *Résumés des sciences aquatiques et halieutiques*, et ils sont classés dans l'index annual des publications scientifiques et techniques du Ministère.

Les numéros 1 à 456 de cette série ont été publiés à titre de rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre. Les rapports épuisés seront fournis contre rétribution par des agents commerciaux.

Canadian Technical Report of
Fisheries and Aquatic Sciences 1567

September 1987

INTERACTIONS BETWEEN ATLANTIC COD (*GADUS MORHUA*) AND CAPELIN (*MALLOTUS VILLOSUS*) OFF LABRADOR AND EASTERN NEWFOUNDLAND: A REVIEW

by

G. R. Lilly

Science Branch
Department of Fisheries and Oceans
P.O. Box 5667
St. John's, Newfoundland A1C 5X1

(c)Minister of Supply and Services Canada 1987

Cat. No. Fs 97-4/1567E ISSN 0706-6473

Correct citation for this publication:

Lilly, G. R. 1987. Interactions between Atlantic cod (Gadus morhua) and capelin (Mallotus villosus) off Labrador and eastern Newfoundland: a review. Can. Tech. Rep. Fish. Aquat. Sci. 1567: vii + 37 p.

CONTENTS

	Page
Abstract	iv
Résumé	v
List of Tables	vi
List of Figures	vii
1. Introduction	1
2. Cod and Capelin Stocks	2
3. The Food of Cod	2
3.1. General feeding pattern	2
3.2. Food of cod off Newfoundland and Labrador	3
3.2.1. Southern Labrador and northeastern Newfoundland (Div. 2J, 3K) offshore	3
3.2.2. Northern Grand Bank (Div. 3L) offshore	5
3.2.3. Southern Grand Bank (Div. 3N, 3O)	6
3.2.4. Inshore	6
3.3. Cod-capelin size relationships	7
4. The Importance of Capelin in the Diet of Cod	7
4.1. Capelin as a proportion of total food	7
4.2. Response of cod feeding to changes in capelin abundance	8
5. Capelin Abundance and Cod Dynamics	11
5.1. Cod growth rate	11
5.2. Cod recruitment and natural mortality	12
6. Quantity of Capelin Consumed	12
6.1. Quantity of capelin consumed by cod	13
6.1.1. Previous estimates of capelin consumption by cod	13
6.1.2. Future estimates of capelin consumption by cod	14
6.2. Quantity of capelin consumed by other predators	15
6.3. Capelin mortality rates due to predation	16
7. Concluding Remarks	16
Acknowledgements	17
References	17

ABSTRACT

Lilly, G. R. 1987. Interactions between Atlantic cod (Gadus morhua) and capelin (Mallotus villosus) off Labrador and eastern Newfoundland: a review. Can. Tech. Rep. Fish. Aquat. Sci. 1567: vii + 37 p.

This paper reviews studies of the interactions between Atlantic cod (Gadus morhua) and capelin (Mallotus villosus) in waters off Labrador and eastern and southern Newfoundland in the northwest Atlantic. Predation by cod on capelin may occur over most of the continental shelf off southern Labrador and eastern Newfoundland and on the Grand Banks of Newfoundland. The intensity of predation, as measured by the quantity of capelin in cod stomachs, varies both spatially and seasonally. Predation occurs primarily in summer and autumn off southern Labrador and northeastern Newfoundland (NAFO Div. 2J3K), but occurs throughout the year on the northern Grand Bank (Div. 3L). Areas and times of intensive predation include the northwestern Grand Bank in spring, the shallow inshore waters of eastern Newfoundland and Labrador in late spring and summer, and Hamilton Bank in autumn.

In offshore areas cod prey upon a wide size range of capelin, but in inshore areas during the capelin spawning season (June-July) they prey predominantly on large (presumably mature) capelin. Capelin is most important for cod of medium length (roughly 40-69 cm).

Several studies have estimated that capelin comprise about 30% of the diet of cod on an annual basis, but these estimates were based on small numbers of stomach examinations with limited spatial and temporal coverage. Extensive quarterly sampling in Div. 3L in 1985 will permit a new estimate of the contribution of capelin to the diet of cod in a specific year in part of the area of concern. Evidence for annual variability comes from a continuing study in autumn in Div. 2J3K, where the intensity of predation by cod on capelin has varied with capelin abundance, and in years of low capelin abundance cod have not compensated by preying more intensively on other prey.

In the only study of the influence of changes in capelin abundance on the productivity of cod, a positive correlation was not found between capelin abundance and the growth of cod. The authors of the study expressed strong reservations about the appropriateness of much of the data. Data for more appropriate tests are being collected.

The quantity of capelin consumed annually by cod has been estimated at 0.8-2.4 times the cod biomass, but these estimates were based on small data sets and involved many untested or invalid assumptions. A new estimate will be made for a part of the area in a single year using quarterly sampling in Div. 3L in 1985. There have been no estimates of the proportion of capelin natural mortality caused by cod predation.

RÉSUMÉ

Lilly, G. R. 1987. Interactions between Atlantic cod (Gadus morhua) and capelin (Mallotus villosus) off Labrador and eastern Newfoundland: a review. Can. Tech. Rep. Fish. Aquat. Sci. 1567: vii + 37 p.

Le présent ouvrage se veut un examen critique des interactions entre la morue franche (Gadus morhua) et le capelan (Mallotus villosus) peuplant les eaux au large du Labrador et des côtes est et sud de Terre-Neuve (Atlantique nord-ouest). La morue peut se nourrir du capelan dans presque toutes les eaux de la plate-forme continentale au large de la côte sud du Labrador, de la côte est de Terre-Neuve et des Grands bancs de Terre-Neuve. L'intensité de la prédation telle que déterminée par la quantité de capelan présente dans les estomacs de morue varie dans l'espace et dans le temps. La prédation a surtout lieu en été et en automne au large de la côte sud du Labrador et de la côte nord-est de Terre-Neuve (div. 2J3KL de l'OPANO), mais se poursuit pendant toute l'année dans les eaux septentrionales des Grands bancs (div. 3L). Les régions et les périodes de prédation intensive comprennent le secteur nord-ouest des Grands bancs au printemps, les eaux côtières peu profondes de l'est de Terre-Neuve et du Labrador à la fin du printemps et en été ainsi que le banc Hamilton en automne.

Dans les régions hauturières, la morue consomme du capelan de diverses longueurs mais dans les régions côtières, elle se nourrit surtout de gros capelans (supposément matures) quand ils frayent (juin-juillet). À titre de source de nourriture, le capelan est surtout important pour les morues de longueur moyenne (environ 40 à 69 cm).

Plusieurs études ont révélé qu'environ 30 % du régime alimentaire annuel de la morue se compose du capelan quoique ces estimations soient basées sur un faible nombre d'échantillons de contenus stomacaux à répartition spatiale et temporelle limitées. Un échantillonnage trimestriel exhaustif de la div. 3L mené en 1985 a permis d'obtenir une nouvelle estimation de l'apport du capelan au régime alimentaire de la morue pendant une année particulière dans une partie du secteur concerné. Une étude prolongée menée en automne dans la div. 2J3KL a révélé une variabilité annuelle; ainsi, l'intensité de la prédation exercée par la morue sur le capelan varie en fonction de l'abondance de ce dernier et, pendant les années de faible abondance du capelan, la morue ne consomme pas de plus grandes quantités d'autres proies.

La seule étude sur l'influence des variations de l'abondance du capelan sur la productivité de la morue n'a pas révélé de corrélation positive entre l'abondance du capelan et la croissance de la morue. Les chercheurs concernés ont exprimé de fortes réserves quant à l'applicabilité de la plus grande partie des données. La cueillette de données qui serviront à des tests plus appropriés est en cours.

Selon des estimations, la morue consomme annuellement de 0,8 à 2,4 fois sa biomasse en capelan quoique ces estimations soient basées sur de petites séries de données et de nombreuses hypothèses invalides et non vérifiées. À l'aide des données recueillies par échantillonnage trimestriel dans la div. 3L en 1985, on établira une nouvelle estimation annuelle pour une partie de la région. On ne dispose pas d'estimations du niveau de mortalité naturelle du capelan résultant de la prédation exercée par la morue.

LIST OF TABLES

		Page
Table 1.	The food of Atlantic cod off southern Labrador and northeastern Newfoundland (NAFO Div. 2J, 3K) in the autumns of 1982 and 1985 (from Lilly 1986)	25
Table 2.	The food of Atlantic cod on the northern Grand Bank (NAFO Div. 3L), May - June, 1979 (from Lilly and Rice 1983)	26
Table 3.	Quantities of capelin in stomachs of the Atlantic cod population in NAFO Div. 2J, 3K at the time of sampling in autumn 1982 (from Lilly 1986).	27
Table 4.	Quantities of capelin (tons) estimated to be present in stomachs of predator populations in Div. 2J,3K at the time of sampling in autumn, 1981-83.	28

LIST OF FIGURES

		Page
Figure 1.	Map of Newfoundland and Labrador, showing NAFO Divisions and localities mentioned in the text.	29
Figure 2.	Changes in total fullness index, and partial fullness indices for major prey, with increasing cod length: Div. 2J3K, autumn 1982 (from Lilly 1984a)	30
Figure 3.	Geographic variation in mean partial fullness index for capelin from cod stomachs in 1981. All stomachs collected from cod (30-69 cm) caught in each 0.5° latitude x 1.0° longitude area were combined. Data from areas with fewer than 5 stomachs were not plotted. Many samples from between approximately 51°00'N and 52°30'N were lost (from Lilly 1984a).	31
Figure 4.	Changes in total fullness index, and partial fullness indices for major prey, with increasing cod length: Div. 3L, May-June 1979 (from Lilly and Rice 1983).	32
Figure 5.	Partial fullness indices of capelin from cod stomachs by fishing set: Div. 3L, May-June 1979 (from Lilly and Rice 1983).	33
Figure 6.	Total fullness index, and partial fullness indices for capelin and squid, in samples of cod collected from the commercial inshore fishery at Trouty, Trinity Bay, during summer 1980 (from Lilly and Osborne 1984).	34
Figure 7.	Length frequency of capelin from stomachs of cod caught in traps at Bonavista, 1983 and 1984.	35
Figure 8.	Length frequency of capelin from stomachs of cod (10 cm length-groups) caught by bottom otter-trawl (Gadus Atlantica trip 49) in northwestern Div. 3L, April 1981.	36
Figure 9.	The prey composition (expressed as fullness index) of Atlantic cod (36-71 cm only) in NAFO Div. 2J+3K in the autumns of 1978 and 1980-85. Arctic cod includes Gadidae. The number of stomachs examined each year is given at the top (from Lilly 1986).	37

1. INTRODUCTION

Capelin (Mallotus villosus) is a major prey of Atlantic cod (Gadus morhua) (hereinafter called cod) off eastern Newfoundland and Labrador (Popova 1962), at West Greenland (Hansen 1949) and Iceland (Palsson 1983), and in the Barents Sea (Grinkevich 1957). The initiation of major fisheries for capelin in several of these areas has presented complex questions regarding simultaneous management of a predator and its prey. There is recognition that removal of too much capelin might result in a decline in cod productivity or a change in cod migration patterns, and that large cod stocks might compete with a commercial capelin fishery. However, in each area the predator and the prey continue to be managed using single species models. This does not mean that management has ignored the interactions. In the Newfoundland-Labrador area, for example, scientists have in recent years advised that total allowable catches of capelin be set at a conservative exploitation rate of 10%, partly out of concern for the effect that harvesting of capelin might have on cod and other predators (Anon. 1982).

Capelin stocks in the Newfoundland-Labrador area suffered dramatic declines in the late 1970's, primarily as a result of a sequence of poor year-classes (Carscadden 1984). Total allowable catches (TAC's) were nil or low through the first half of the 1980's (Anon. 1986; Carscadden and Atkinson 1986). However, the stocks appear to be recovering (Carscadden 1986; Carscadden and Atkinson 1986; Miller 1986), and it is possible that requests for much larger quotas will be forthcoming. Is the 10% exploitation rule adequate, or should we attempt to understand the predator-prey interaction more thoroughly in hope that such knowledge will permit the selection of an overall pattern of fishing which optimizes economic and social benefits. Decisions on the quantity, location and timing of the harvest of each species will be based largely on economic and social considerations, but a sound understanding of the ecology of the two species is essential for determining what trade-offs are involved in terms of total catch, catch rate, variability in supply, and so on. (For further discussion of the types of trade-offs involved, see Gulland (1982, 1983) and Clark (1985), both of whom cite cod-capelin fisheries as examples of multispecies fisheries which must involve trade-offs.)

The purpose of this paper is to consolidate and evaluate most of the published information on the trophic interactions between cod and capelin in the Newfoundland-Labrador area. Much of this information is available only in mimeographed research documents of the International Commission for the Northwest Atlantic Fisheries (ICNAF) and its successor, the Northwest Atlantic Fisheries Organization (NAFO). In addition, I shall present preliminary analyses of some unpublished material, and outline briefly some of the studies in progress.

This paper was originally prepared as a discussion document for a session on cod-capelin interactions during the autumn 1985 meeting of the Marine Environmental and Ecosystem Subcommittee of the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC). A second paper presented at that meeting (Lear et al. 1986) contains discussion and preliminary examination of the influence of capelin on the migration of cod from offshore waters to the

inshore area of southern Labrador and eastern Newfoundland (NAFO Div. 2J, 3K, 3L).

2. COD AND CAPELIN STOCKS

Although cod feed on capelin in the Gulf of St. Lawrence (Minet and Perodou 1978; Nakashima et al. 1982; Waiwood and Majkowski 1984) and off the south coast of Newfoundland (Popova 1962; Stanek 1975; Minet and Perodou 1978), the area of major concern in Atlantic Canada has been from central Labrador to the southern Grand Bank (Fig. 1). Stocks of interest are the 2+3K, 3L, and 3NO capelin stocks, and the 2J+3KL and 3NO cod stocks.

A major problem with assessing interactions is immediately apparent: stock boundaries do not coincide. Thus, the 2J+3KL cod stock presumably preys on both the 2+3K capelin stock and the 3L capelin stock. Indeed, it is even more complicated than this, for both cod and capelin have seasonal migrations associated with spawning and feeding, and these migrations often cross boundaries between divisions. For example, the 3NO capelin stock is thought to overwinter in Div. 3L (Winters and Carscadden 1978), so the 2J+3KL cod stock probably preys on all three capelin stocks.

In addition, the 2J+3KL cod stock comprises several components (Lear 1984a), each of which probably overlaps with capelin stocks in a manner distinct from the other components. Northern components may prey primarily on the 2+3K capelin stock, central components may prey on the 2+3K and 3L capelin stocks, and southern components may prey on the 3L and 3NO capelin stocks. An additional complication is the different distributions exhibited by mature and immature capelin of the same stock, particularly near spawning time.

The migration patterns and other aspects of the biology of the cod and capelin stocks will not be reviewed here. Both species were reviewed by Templeman (1966) and Pinhorn (1976), and a brief review of the northern stocks of both species was provided by Akenhead et al. (1982). Additional reviews include those by Jangaard (1974) and Carscadden (1984) for capelin and Lear (1986) for cod.

3. THE FOOD OF COD

3.1. GENERAL FEEDING PATTERN

Cod are considered to be demersal fish, but in most geographic areas a high proportion of their prey are taken from the plankton and nekton. A very wide variety of taxa are eaten, but major prey are usually crustaceans and fish. Small cod tend to feed on small crustaceans, such as mysids, euphausiids, amphipods, and small shrimp; medium-sized cod feed on larger crustaceans and small fish, especially pelagic fish; and large cod feed on crabs and medium-sized fish, such as pleuronectids (see, for example, Powles (1958) and Waiwood and Majkowski (1984) for the Gulf of St. Lawrence; Minet and Perodou (1978) and Lilly and Fleming (1981) for eastern Newfoundland; Palsson (1983) for Iceland; and Rae (1967) and Daan (1973) for the North Sea). Within

a given prey taxon, there is a tendency for the median prey size to increase with increasing cod size (see Lilly (1984b) for predation on shrimp and crabs and Palsson (1983) for predation on capelin and redfish).

An increase in prey size with increasing predator length is thought to be a consequence of energetic advantages associated with the selection of large prey (Kerr 1971; Wankowski and Thorpe 1979) and a morphological limitation on maximum prey size (Wankowski 1979). However, as noted by Lilly and Rice (1983) and others, prey size is not the only factor influencing prey selection. There have been many occasions when high numbers of small prey have been found in stomachs of large cod. For example, several thousand euphausiids have occasionally been found in stomachs of cod >80 cm in length (Lilly and Rice 1983), and several hundred small (5-7 cm) capelin have occasionally been found in stomachs of large cod, the highest number to date being 1650 in a 121-cm cod (G. Lilly unpubl. data). Such incidences support an hypothesis that abundance (or availability) of prey is important in prey selection by cod, as it is in other predatory fish (Allan 1981).

3.2. FOOD OF COD OFF NEWFOUNDLAND AND LABRADOR

3.2.1. Southern Labrador and Northeastern Newfoundland (Div. 2J,3K) offshore

As discussed by Lilly et al. (1984), there are major differences in the reported patterns of predation by cod on capelin offshore in Div. 2J,3K. Minet and Perodou (1978) reported that in Div. 2J capelin was the major prey (55% by weight) of cod in winter but a very minor prey (<1%) in summer. Turuk (1968) found the opposite; cod fed poorly, primarily on invertebrates, in winter and spring but fed more intensively, primarily on capelin, in summer and autumn. Turuk's (1968) observations are supported by Templeman (1965) for the spring, by Popova (1962) and Templeman (1965) for the summer, and by Lilly (1984a; 1986) for the autumn. For Div. 3K, Minet and Perodou (1978) found that in summer capelin was a minor prey of cod, whereas Popova (1962) and Turuk (1968) found it to be a major prey, at least in some areas. Both Minet and Perodou (1978) and Turuk (1968) found capelin to be a minor prey in Div. 3K in winter.

There have been no further studies of cod feeding in this area in summer, so the differences at this season between the observations of Minet and Perodou (1978) and those of other authors remain unresolved and puzzling. There has, however, been an attempt to study feeding during winter (February-April) by collecting stomachs opportunistically during research surveys and tagging operations and from catches of commercial trawlers (Lilly et al. 1984). Results of these recent collections agree with Templeman (1965) and Turuk (1968) that the intensity of feeding on capelin and other prey is low. The distribution of capelin in winter is poorly understood. In autumn the capelin are primarily on central Hamilton Bank and southward on or near the coastal shelf (Kovalyov and Kudrin 1973), and there is apparently a southward migration during the autumn (see also Bakanev and Gorchinsky 1985). Thus, in winter most of the capelin are probably to the west and southwest of the cod, which are concentrated near the outer edge of the continental shelf (Lear 1984b). The few capelin reported by Lilly et al. (1984) were found in stomachs of cod caught on the central part of Belle Isle Bank and western Funk Island Bank.

Sampling in Div. 2J by Minet and Perodou (1978) was apparently confined to Belle Isle Bank (see their Fig. 1), whereas sampling by Templeman (1965) was confined to Hamilton Bank and that reported by Turuk (1968) may have been conducted primarily on southern and southeastern Hamilton Bank. Thus, the difference between the diet reported by Minet and Perodou (1978) and that reported by other authors may have been due to differences in study area. It is also possible that the capelin were distributed more widely than usual when Minet and Perodou sampled in winter 1975, for the very strong 1973 year-class would have been very abundant at that time.

The most intensive and extensive examination of cod feeding in Div. 2J+3K has come from collections during stratified-random bottom-trawl surveys conducted annually in autumn since 1978 (Lilly 1984a, 1986). The prey spectrum was very similar in two selected years, 1982 and 1985 (Table 1). Fish and crustaceans were dominant. The most important fish in both years was capelin, but Arctic cod (Boreogadus saida), flatfishes (F. Pleuronectidae), eelpouts (F. Zoarcidae) and redfish (Sebastes sp.) were also important in one or both years. Unidentified fish was a large proportion (21% by weight) of the stomach contents in both years. The major crustacea in terms of weight were shrimp, mainly Pandalus borealis, and crabs, mainly Chionoecetes opilio. Several invertebrate groups, such as polychaetes, gammarid amphipods, mysids, and euphausiids, occurred frequently but were not important in terms of weight. Hyperiid amphipods occurred more frequently and contributed far more to stomach content weight in 1985 than in 1982. The prey composition was very similar in other years, but the relative importance of some of the groups varied, as will be discussed later.

The relative importance of the various prey in 1982 varied with cod length (Fig. 2). Capelin was important for all but the smallest cod (<25 cm), and flatfish and eelpouts were consumed mainly by large cod (>75cm). The cod which might be most affected by changes in capelin abundance are those within the length range for which capelin is the most important prey. This length range appears to be roughly 30-69cm in this area at this time of year.

Spatial variability in predation on capelin in autumn 1981 is shown in Fig. 3. Partial fullness indices were highest on Hamilton Bank, but capelin were also found in cod on Harrison Bank to the northwest of Hamilton Bank, on or near the coastal shelf off southern Labrador and northeastern Newfoundland, and on Funk Island Bank. Patterns in other years were similar.

The following summary of the seasonal pattern in Div. 2J, 3K is quoted from Akenhead et al. (1982). During the January-May period when the cod are concentrated in warm, deep water they feed at low intensity on invertebrates, but as they move into shallower water and toward shore in early summer they feed intensively on capelin. Predation on capelin remains high in early autumn, but becomes less intense toward December as the cod return toward the slope. The distinct seasonality in feeding and the presumed importance of capelin in the annual cycle are supported by observation that the cod livers enlarge quickly in summer, remain large through the autumn, and decline through winter and spring to a low in May-June (Turuk 1968).

3.2.2. Northern Grand Bank (Div. 3L) Offshore

Predation by cod on capelin is not as seasonal in Div. 3L as it is to the north. Cod on the northern slopes of Grand Bank feed on capelin in winter (Templeman 1965; Turuk 1968; Minet and Perodou 1978; Lilly et al. 1984), and partial fullness indices can be very high (Lilly and Fleming 1981). Cod also feed on capelin in various parts of the Avalon Channel and the northern, western, and central Grand Bank in spring and summer (Popova 1962; Turuk 1968; Kovalyov and Kudrin 1973; Stanek 1975; Minet and Perodou 1978; Lilly and Fleming 1981). Predation on capelin also occurs in autumn (Turuk 1968), but there has been less study at that season.

The results of a study of cod feeding in Div. 3L in May-June, 1979 were reported by Lilly and Rice (1983). As in Div. 2J3K, the cod preyed upon a wide variety of organisms, but only a few species were important in terms of weight (Table 2). Sand lance (Ammodytes sp.) and capelin comprised 43% of the diet by weight, and other fish plus unidentified fish comprised an additional 11%. The most important crustacea were crabs (Chionoecetes opilio and Hyas araneus), euphausiids (predominantly Thysanoessa raschii), shrimp (mainly Pandalus montagui), and gammarid and hyperiid amphipods. The intensity of predation on major prey categories, as determined from mean partial fullness indices, varied with cod length (Fig. 4). Euphausiids were preyed upon most intensively by small cod; sand lance and capelin by medium-sized cod (40-69 cm); crabs by large cod (60-79 cm); and flatfish by the largest cod (>80 cm). However, each prey category was preyed upon by a wide size range of cod, and there were no abrupt changes in diet with increasing cod length.

In May-June 1979 capelin were found in cod stomachs in most fishing sets from the western and central parts of Div. 3L (Fig. 5). Partial fullness indices were highest north of the Virgin Rocks. Capelin were not found in cod stomachs collected on the eastern Grand Bank, and in many sets north of the Bank. The major prey in the eastern area was sand lance, which was the major prey in this area in the summers of 1966 and 1967 as well (Lilly and Fleming 1981).

In some years the spatial pattern of cod predation on capelin in spring was different from that found in 1979. Partial fullness indices were sometimes low in the central area and highest in the north and east (Lilly and Carscadden 1986). Possible contributors to differences among years include differences in migration patterns of capelin, differences in relative abundance of juvenile and maturing capelin, and differences in timing of the surveys.

A detailed set-by-set examination of the data reported in Lilly and Carscadden (1986) and additional cod stomach content data collected in 1985 and 1986 is expected to provide a clearer understanding of the seasonal and annual variation in the distribution of cod and capelin, and the intensity of predation by cod on capelin.

3.2.3. Southern Grand Bank (Div. 3N, 3O)

As noted by Lilly et al. (1981), predation by cod on capelin in Div. 3NO appears to occur primarily in spring and summer, although this may simply reflect a low level of study in autumn and winter. Capelin have been reported in cod stomachs in Div. 3O, particularly near the southwest slope, from March to June (Martin and Costa 1954; Kovalyov and Kudrin 1973; Bulatova 1973; Stanek 1975), and in Div. 3N near the Southeast Shoal in June-July (Martin and Lucio 1955; Martin 1956; Templeman 1965; Bulatova 1973). These observations are in agreement with the reported migration of capelin through Div. 3O to the Southeast Shoal in Div. 3N, where they spawn in June-July (Kovalyov and Kudrin 1973). In summer 1959-60 capelin was a minor component of the cod diet in both Div. 3O and Div. 3N. The major prey at that time was sand lance (Popova 1962). Sand lance was also the major prey of cod studied at various seasons in 1965-70 and 1978 in a single area of the eastern slope of Grand Bank (Lilly 1982). Cod stomachs were collected throughout Div. 3NO during bottom-trawl surveys in spring 1984-86 and in an area just west of the Southeast Shoal in late autumn 1983. Capelin were found in cod stomachs during all these surveys, but sand lance was much more important (Lilly and Meron 1986; G. Lilly unpubl. data).

3.2.4. Inshore

Cod migrate to the shallow inshore waters of southern Labrador and eastern Newfoundland (Div. 2J, 3K, 3L) during late spring and summer and feed intensively on capelin which have approached the coast to spawn (Thompson 1943). The migration and factors which might affect the proportion of cod coming inshore were discussed by Lear et al. (1986).

As noted by Lilly and Botta (1984), there are very few published studies of the food of cod in inshore areas. Templeman (1965) described the relative importance (as percentage of total volume of stomach contents) of major prey of cod caught in the shallow-water fishery at St. John's from May to November, 1947-51. From mid-June to early August the cod fed almost entirely on capelin, whereas from mid-August to late November they fed mainly on bottom invertebrates, especially crustacea. Lilly and Fleming (1981) reported that capelin represented 99% by weight of the stomach contents of cod from traps (poundnets) at St. John's and Bonavista in July, 1968-69.

Lilly and Botta (1984) reported preliminary results of studies at Bonavista in 1983. Cod caught in traps in late June and July had fed intensively and almost exclusively on capelin, whereas cod caught after July by other gears had fed much less intensively, primarily on benthic invertebrates. Similar results were reported by Lilly and Osborne (1984), who studied the food of cod at Trouty, Trinity Bay, in summer 1980 (Fig. 6). Largest quantities of capelin were found in stomachs of cod caught in traps from late June to early July, and smaller but still large quantities were found in cod from traps in mid-July and gillnets in late July. There was very little natural food in stomachs of cod caught on handlines in August. At nearby Trinity large quantities of capelin were found in stomachs of cod caught in gillnets in early July 1982 (G. Lilly unpubl. data). Thus, although an examination of seasonal changes in feeding intensity will be confounded at many locations by a

mid-summer change in commercial fishing gear (from traps to hook and line), it appears that there is not much food for cod in the inshore area after the capelin die or move offshore following spawning.

There have been several intensive studies of cod stomachs in recent years by DFO, university scientists, and commercial companies under contract, so our understanding of seasonal, annual, and geographic variability in cod feeding in inshore waters should improve in the next few years.

3.3. COD-CAPELIN SIZE RELATIONSHIPS

The size range of cod that prey on capelin is not easily defined (Lilly and Fleming 1981). Cod must be about 35 cm in length to feed on adult capelin, but cod as small as 20 cm can feed on juvenile capelin. Cod with the highest partial fullness indices for capelin tend to be in the range 40-69 cm, but the upper limit in particular is highly variable.

In the inshore area during the capelin spawning period the cod feed almost entirely on large capelin (Fig. 7), which are probably predominantly mature. However, in offshore areas there may be intensive predation on juveniles. For example, cod collected in northern Div. 3L in April 1981 were preying on capelin ranging from 8 to 18 cm (Fig. 8). A mode at 11 cm, which was most prominent in capelin from stomachs of medium-sized cod, corresponds to a mode at 11-12 cm in the catches of an acoustic capelin survey in this area in June 1981 (Miller et al. 1982). The capelin from the acoustic survey were determined by age-reading of scales to be 2-year-olds. In April 1981 the modal length of capelin prey increased with increasing cod length, but even large cod fed on small capelin (Fig. 8). Predation on 10-12 cm capelin has also been reported by Popova (1962) and Templeman (1965). Age 1 capelin (6-7 cm) have been found in cod stomachs in the spring in Div. 3L and Div. 3NO, and even 0-group capelin (5 cm) have been found in cod stomachs collected in late autumn in Div. 3N (G. Lilly unpubl. data).

4. THE IMPORTANCE OF CAPELIN IN THE DIET OF COD

4.1. CAPELIN AS A PROPORTION OF TOTAL FOOD

As noted by Lilly et al. (1981), the proportion of capelin in the diet of cod has not been investigated in a large geographic area on an annual basis, but observations from limited spatial and seasonal coverage are available. Templeman (1965) reported that capelin comprised 55% by volume of the food of cod taken from May to November in the inshore fishery at St. John's. Campbell and Winters (1973) estimated that capelin comprised 32% by volume of the food of cod on an annual basis. This estimate was derived from an unspecified analysis of data obtained from Templeman (1965; pers. comm.) on the food of cod collected from various gears in Div. 2J+3KLNO. Minet and Perodou (1978) found that capelin comprised 56% of the diet of offshore cod in Div. 2J3KL during the winter and summer. They assumed that no capelin are consumed during spring and autumn, and thereby estimated that capelin comprise 28% of the annual food consumption. They cautioned that this would be a minimum figure, since cod

would eat some capelin in spring and autumn, and the intense predation inshore in summer was not included in the sampling. Additional reasons for caution are the limited spatial coverage in each season, the small number of stomachs examined, and the differences between their observations of cod feeding and the patterns reported by other investigators (see Section 3.2.1).

The proportion of capelin in the diet of cod is also available from more recent sampling. For example, capelin was 16% and 36% by weight of the stomach contents of cod collected in Div. 2J, 3K during the autumns of 1982 and 1985 respectively (Table 1) and 15% by weight of the stomach contents of cod collected in Div. 3L in spring 1979 (Table 2). These values are simply percentages calculated from all the stomachs collected in single surveys, and may be very different from a final estimate of capelin as a percentage of annual food consumption by the cod stock. For each survey, some of the unidentified fish should be allocated to capelin, the various prey should be weighted for different gut evacuation times (MacDonald et al. 1982), and the calculations should involve stratification by area and cod length. Information from other seasons must be incorporated, and the intensive predation on capelin by a portion of the cod stock in inshore areas during spring and early summer must be included. Our first calculation of the contribution of capelin to the diet of cod in a specific year will be based on intensive quarterly sampling on the northern Grand Bank (Div. 3L) in 1985.

4.2. RESPONSE OF COD FEEDING TO CHANGES IN CAPELIN ABUNDANCE

Calculation of the contribution of capelin to the total food intake of cod in a specific year will provide some indication of the importance of capelin to cod, but one really needs to know how the feeding and productivity of cod vary in response to changes in capelin abundance. It is impractical to conduct an experiment in which wild populations of cod are maintained at several combinations of cod and capelin abundance in order to study the relationship between the feeding rate of cod and the per capita availability of capelin. An alternative approach, slow but potentially rewarding, is to monitor the abundance of capelin and the feeding of cod under natural conditions. As capelin change in abundance, and they will even in the absence of a fishery, the diet of cod can be examined to determine the relationship between predation rate and capelin abundance (functional feeding response to prey density). (A difficulty is that cod abundance will also vary, and there may be a functional response to predator density.) As capelin abundance declines from maximum values, there will at some point be a decline in the rate of consumption of capelin by cod, and this might result in a decrease of the same magnitude in the total rate of food consumption, or might be compensated for, in whole or in part, by predation on other prey. Certain species of alternate prey could increase in abundance as a consequence of the capelin decline because they are either competitors or prey of capelin.

The influence of changes in capelin abundance on the feeding of cod may be investigated in the autumn in Div. 2J, 3K, where there are annual collections of cod stomachs during stratified-random bottom-trawl surveys (see Section 3.2.1.) and estimates of capelin abundance from acoustic surveys and the analysis of commercial catch rates. Such data do not lend themselves to

the study of either a true functional feeding response or an aggregative numerical response, because synoptic measures of density of cod and capelin, together with cod feeding data, would be difficult to extract on fine spatial scales. For an initial examination, Lilly (1986) simply calculated an unweighted mean stomach fullness index for cod collected throughout Div. 2J, 3K in each year, and compared these means to estimates of total capelin abundance. Because capelin is the major prey for only medium-sized cod (Lilly 1984a), the analysis was restricted to cod in the length range 36-71 cm. Data were available for 1978 and 1980-85.

The total fullness index varied from 0.94 in 1978 to 2.58 in 1985 (Fig. 9). Most of the variability was due to capelin, which rose from a very low level in 1978 to a peak in 1981, declined in 1982 and 1983, and then increased again in 1984 and 1985. A large proportion of the fish was unidentified, and much of this was probably capelin. Estimates of capelin abundance are available from acoustic surveys conducted by both the USSR and Canada (Lilly 1986). The USSR did not conduct a survey in 1981, and the Canadian series started in 1981 and excluded 1982. For the three years of overlap (1983-85) correspondence between the estimates was not good ($r = 0.53$). The PFI for capelin was positively correlated with the USSR acoustic biomass estimates but not with the Canadian estimates (Lilly 1986). A tentative conclusion from this analysis is that the quantity of capelin in cod stomachs reflects the annual variability in capelin abundance. However, the relationship is not well described. A continuation of the monitoring is necessary. Good stomach sampling during years of low capelin abundance is critical. An additional problem with describing the relationship is obtaining reliable measures of capelin abundance, for there are recognized problems with all methods currently in use, and the various indices are not highly correlated (Carscadden et al. 1985).

A critical question is whether cod prey more intensively on other prey when capelin availability is reduced (Akenhead et al. 1982). In this short time series the PFI for all other prey combined was not negatively correlated with the PFI for capelin (Lilly 1986). The alternate prey include benthic species, the most important of which are shrimp (mainly Pandalus borealis) and crabs (mainly Chionoecetes opilio), and pelagic species, the most important of which are hyperiid amphipods and Arctic cod. The PFI for shrimps and crabs remained relatively invariable over time (Fig. 9), so there is no indication of an increase in feeding on these groups during years of low capelin abundance. In contrast, the PFI values for hyperiids and Arctic cod were more variable, and these two prey will be discussed in more detail.

Hyperiids are major prey of capelin in Div. 2J (Chan and Carscadden 1976). Lilly (1984a) noted the decline of hyperiids in cod stomachs during the period 1978-82 (Fig. 9), assumed that this decline reflected a decline in hyperiid standing stock, and postulated that hyperiid abundance may have increased under reduced predation pressure from capelin in the late 1970's and then declined in the early 1980's as capelin biomass increased. However, the PFI for hyperiids increased once again from 1982 to 1985, even though the biomass of capelin remained high and reached the highest level in the series in 1985. The increase in predation on hyperiids was very pronounced on Hamilton Bank, where capelin abundance was highest (Lilly 1986). There is thus no

evidence from this time series that cod feed more heavily on hyperiids when capelin abundance is low.

Arctic cod is a planktivore which, like capelin, feeds largely on calanoid copepods and hyperiids (Lilly, 1980). It is possible that Arctic cod were more successful when capelin abundance was low, and that the greater feeding rate by Atlantic cod on Arctic cod during 1978 and 1980 compared with 1981-83 (Fig. 9) may reflect a higher absolute abundance of Arctic cod in the earlier years. Alternatively, the greater feeding rate on Arctic cod in 1978 and 1980 may simply reflect the high relative abundance of Arctic cod in the pelagic fish community noted during acoustic surveys by Canada in 1978-1980 (Miller 1979; Carscadden and Miller 1980; Miller and Carscadden 1981), and by the USSR in 1978 and 1980 (Seliverstov and Serebrov 1979; Bakanev 1981). Additional evidence for a high relative abundance of Arctic cod was the high by-catch of this species in the Romanian capelin fishery in 1979 (Maxim 1980). The high relative abundance of Arctic cod in 1978-80 could have resulted from a severe reduction in capelin abundance with no absolute increase in Arctic cod abundance. Weak support for this comes from biomass levels of Arctic cod estimated from catches during bottom-trawl surveys (Lear and Baird 1985). The biomass estimates fluctuated from year to year, with no correlation between divisions. There is no indication that biomass was higher in 1978-80 than in 1981-83. Predation by Atlantic cod on Arctic cod increased again in 1984 and especially in 1985, when predation on capelin was high. There is therefore no support for an inverse relationship between predation on capelin and predation on Arctic cod (Lilly 1986). Most of the Arctic cod found in Atlantic cod stomachs came from two length-groups with modes at 5 cm and 9-11 cm (G. Lilly unpubl. data). These modes correspond to ages 0 and 1 (Lear 1979; Miller 1979; Wells 1980). Thus, annual variability in intensity of predation by Atlantic cod on Arctic cod could reflect changes in year-class strength of Arctic cod. Alternatively, the annual variability in predation on Arctic cod might result from a southward shift of the Arctic cod population in some years. It is curious that Arctic cod are not mentioned in reports of cod stomach examinations in this area during the 1960's (Popova 1962; Templeman 1965; Templeman and May 1965; Turuk 1968; Stanek 1973) and the mid-1970's (Minet and Perodou 1978).

Several tentative conclusions may be drawn from this short series of cod stomach examinations in Div. 2J, 3K in autumn. The rate of predation by cod on capelin varied with capelin abundance. At times of low capelin abundance cod did not compensate by preying more intensively on other prey. Two pelagic prey (hyperiids and Arctic cod) are preyed upon with varying intensity. If the intensity of cod predation on these prey is a reflection of their abundance, then it appears that their abundance is not strongly influenced by interactions with capelin.

Because the feeding rate of cod on capelin varies with capelin abundance, and cod apparently do not feed more intensively on other prey in years of low capelin abundance, one might predict that the interannual variability in capelin abundance would be reflected in changes in cod vital rates, such as growth rate, fecundity, age (or size) at maturity, and mortality. The changes might be more pronounced in Div. 2J than in Div. 3K because capelin concentrate on Hamilton Bank and the coastal shelf just to the south, at least in the

autumn. However, the rate of feeding by cod in autumn may not be a good index of the rate of energy accumulation by cod throughout the year. For example, during the preceding spring and early summer cod would have preyed on maturing capelin both offshore and inshore. The rate of consumption of maturing capelin offshore will probably increase with the magnitude of the maturing biomass. The rate of consumption inshore may be less dependent on the magnitude of the mature biomass, because the mature capelin are highly aggregated in a relatively small area close to shore just prior to and during spawning. Additional variability may be caused by variability in the proportion of the cod stock coming inshore. The proportion coming inshore might be affected by the magnitude of the mature capelin biomass and by other factors, such as the temperature of the Labrador Current (Lear et al. 1986). Thus, an examination of the influence of capelin abundance on cod vital rates will require information on the abundance of capelin both before and after capelin spawning. Deriviation of an adequate index of capelin availability will require not only improved understanding of the feeding behaviour of cod in autumn, but also some knowledge of the intensity and variability of cod predation on capelin in spring and summer, both offshore and inshore.

A series of stomach examinations in spring or autumn is not yet available for Grand Bank. There the major alternate prey is sand lance, which has experienced changes in abundance in recent decades (Winters 1983). Other important prey are euphausiids and crabs. Any examination of annual variability in cod feeding on Grand Bank should also examine the role of squid (Illex illecebrosus), which might be an important prey for large cod in some years (Lilly and Osborne 1984).

5. CAPELIN ABUNDANCE AND COD DYNAMICS

5.1. COD GROWTH RATE

If the per capita food consumption of cod increases with capelin abundance, one would predict that the growth rate of cod would also increase with capelin abundance. Akenhead et al. (1982) used correlation analysis to determine if there was any relationship between cod growth and capelin biomass, cod biomass, and water temperature. The growth data were mean annual length increments of cod caught in traps in Div. 2J, 3K, and 3L in the period 1970-78. Capelin abundance indices were available for the 2+3K capelin stock, and water temperatures were taken from Station 27 off St. John's. No statistically significant relationships were found. However, the authors expressed strong reservations about the appropriateness of much of their data. For example, determinations of cod length-at-age were from cod sampled at varying locations at varying times during the inshore period, when cod are feeding intensively and presumably growing very rapidly.

A more appropriate test of the relationship between cod growth and capelin abundance might be formulated from data collected during the autumn bottom-trawl surveys in Div. 2J, 3K. The cod in this area spawn in March-April, feed most intensively in summer and autumn, and appear to be at peak condition during autumn (see Section 3.2.1). Thus, the timing of the surveys (late October to early December) may be appropriate for measuring

length-at-age, somatic weight, gonad weight, and liver weight near the end of the growth period. These variables have been measured each year. Stomachs have been collected. Capelin abundance has been estimated by a variety of methods, including an acoustic survey just prior to the bottom-trawl survey. It remains to be determined if the sampling design and intensity are adequate for testing multispecies hypotheses.

5.2. COD RECRUITMENT AND NATURAL MORTALITY

There are several ways in which capelin abundance might affect cod recruitment.

For a given cod stock abundance, it is possible that egg production by the stock will increase with capelin abundance. This is because per capita food consumption may be a function of capelin abundance (see Section 4.2), and with increasing food consumption one would predict an increase in growth rate, and possibly a decrease in age at maturity and an increase in size-specific fecundity, all of which will increase egg production by the stock. However, the relationship between egg production and recruitment is not clear.

Survival of cod eggs and larvae may decrease with increasing capelin abundance if capelin consume cod eggs and larvae or if cod larvae and capelin larvae compete for food.

Survival of juvenile cod may increase with increasing capelin abundance if the rate of predation on juvenile cod by larger cod or other predators (e.g. squid) is inversely proportional to capelin abundance. In contrast, survival of juvenile cod may decrease with increasing capelin abundance if capelin and juvenile cod compete for food.

The ability of adult cod to survive overwintering and spawning may increase with capelin abundance because of increased energy reserves accumulated during more intensive feeding on capelin during the previous feeding season.

To my knowledge, none of the possible interactions described in this section has been investigated. Each might be important in influencing production by cod in the long-term.

6. QUANTITY OF CAPELIN CONSUMED

Estimates of the consumption of capelin by cod and other predators are necessary if one intends to allocate portions of the available capelin biomass to predators and to a fishery, and leave sufficient spawning stock to ensure that recruitment is not impaired. In addition, information on consumption of individual year-classes of capelin will help determine the relationship between the number of capelin surviving the larval stage and ultimate recruitment to the fishery. In other words, it will help reveal the extent to which predation on juvenile capelin affects recruitment to the capelin fishery.

6.1. QUANTITY OF CAPELIN CONSUMED BY COD

As noted by Lilly et al. (1981), there are two basic ways of estimating the quantity of a specific prey consumed by a species of predator. A direct method is to measure the quantity of that prey in the stomachs of the predators, and to estimate feeding rate by applying estimates of the rate of passage of the prey through the predators' guts. An indirect method is to estimate total consumption by the predators from a metabolic model and empirical data on production, and to assign a portion of the total consumption to the prey under consideration on the basis of that prey's contribution to the total stomach contents of the predators. Both methods require quantitative observations of the stomach contents of the predator species throughout its range over the time period for which the estimates are made.

6.1.1. Previous Estimates of Capelin Consumption by Cod

The quantity of capelin consumed annually by cod has been estimated by Winters and Carscadden (1978), Minet and Perodou (1978), and Turuk (1978). The following review of these studies is taken from Lilly et al. (1981).

Winters and Carscadden (1978) estimated the annual consumption of food per unit weight of cod in unexploited cod stocks by assuming that for a population in equilibrium, the production-biomass ratio (P/B) is equal to the total mortality coefficient (Z). Since consumption (C) may be calculated from P/K, where K is gross growth efficiency, then consumption may be estimated as:

$$C = P/K = BZ/K.$$

Consumption of capelin per unit biomass of cod is:

$$C/B = (P_c BZ)/(KB),$$

where P_c is the proportion of capelin in the cod diet. By assuming P_c=0.32 (Campbell and Winters 1973), Z=0.2, and K=0.1, Winters and Carscadden (1978) calculated that the annual consumption of capelin per unit weight of cod was 0.64. They then assumed, however, that at the reduced level of cod abundance in the late 1960's the upper limit of the range given by Campbell and Winters (1973) might be more applicable. Campbell and Winters (1973) had stated that "from preliminary data collected on the food of cod in Div. 3L, it appears that, on the average, cod consume from 0.5 to 1.0 times their own weight in capelin annually". The derivation of this consumption rate was not given.

Minet and Perodou (1978) used a direct method of estimating consumption rates of cod in Div. 2J3KL. They assumed that cod ate in discrete meals and estimated from empirical data the mean weight of capelin in the meal of an average cod. From published information on gastric evacuation rate, they calculated the number of meals of capelin per year. They further assumed that cod prey on capelin for only half the year (summer and winter), and concluded that the average cod consumed from 0.76 to 1.27 times its weight of capelin

annually. These estimates should be treated with caution for reasons stated in Section 4.1.

Turuk (1978) also used a direct method. She combined estimates of feeding rate with observations on stomach contents for cod in Subarea 2 and Div. 3NO. The daily feeding rates of cod in Div. 2GHJ and Div. 3NO were stated to be 3.17% and 7.28% of body mass respectively (source unstated). These feeding rates seem high. The period of intensive predation was reported to be 4 months (August-November) in Div. 2GHJ and 3 months (May-July) in Div. 3NO. Turuk first assumed that during these periods the cod fed entirely on capelin, and thereby calculated that the minimum annual consumption of capelin by cod was 3.8 times the cod biomass in Div. 2GHJ and 6.5 times the cod biomass in Div. 3NO. However, the frequency of occurrence of capelin in cod stomachs containing food was only 65% in Div. 2GHJ and 35% in Div. 3NO. Turuk indicated that these values should be used to correct the above estimates of capelin consumption. Such a correction is inappropriate, since it uses percent occurrence rather than percent weight, but when applied it yields values of 2.47 and 2.29 for the weight of capelin eaten per unit weight of cod in Div. 2GHJ and Div. 3NO respectively. (Note that Turuk did not make this change correctly in her Table 2.) The average of these values is 2.38.

The above estimates of the consumption of capelin per unit biomass of cod range from 0.8 to 2.38. Thus, at a biomass of 1 million t (approximate 4+ biomass in 1982, Baird and Bishop (1986)), the 2J3KL cod stock would consume 0.8 to 2.4 million tons of capelin. The above estimates must be treated with caution, however, for each involves many untested or invalid assumptions and each lacks the extensive spatial and temporal sampling required to characterize the annual diet of the cod. In addition, such estimates cannot consider annual variability in capelin consumption resulting from variability in capelin availability.

6.1.2. Future Estimates of Capelin Consumption by Cod

An attempt can be made to determine the quantity of capelin consumed by cod in Div. 3L, based on quarterly sampling in 1985 of stomach contents, length-at-age, and weights of body components. Two methods can be used: the direct approach using stomach contents and information on gastric evacuation rate, and an indirect approach using a metabolic-based model (eg. Majkowski and Waiwood 1981; Jobling 1982; Kerr 1982; Majkowski and Hearn 1984).

The direct approach is illustrated using data from the 1982 autumn bottom-trawl survey in Div. 2J, 3K (Table 3). The weight of capelin in the stomachs of the cod population at the time of sampling in Div. i (W_i) was estimated as:

$$W_i = \sum_{j=i}^{n} S_{ij} N_{ij}$$

where S_{ij} is the mean weight of capelin in the stomachs of cod of length-group j, N_{ij} is the number of cod of length-group j in the population, and n is the

number of 9-cm length-groups. S_{ij} is the unweighted mean weight of capelin in the stomachs examined; there is no weighting by catch or stratum. N_{ij} was calculated by areal expansion of the stratified arithmetic mean number per 3-cm length-group per tow (Smith and Somerton 1981) using strata defined in Doubleday (1981). Numbers per 3 cm group were combined into 9 cm groups. Cod of intermediate size (54-71cm) had the greatest quantity of capelin in their stomachs (Table 3). Similar patterns were seen in 1981 and 1983. The total quantity of capelin estimated to be present in stomachs of the cod population at the time of sampling was 941 t. Larger quantities were estimated to be present in 1981 and 1983 (Table 4).

Such estimates of the quantity of capelin present in cod stomachs at the moment of sampling are expected to have considerable imprecision and unknown accuracy. The estimates of the average weight of capelin in the stomachs (S_{ij}) can be improved by considering spatial variability more explicitly and by weighting for catch, but variances are expected to be high. The estimates of cod abundance (N_{ij}) are known to have high variances, and probably underestimate actual abundance. For example, Sinclair et al. (1984) found that the ratio between the biomass estimated from surveys and that estimated from cohort analysis was on average 0.47 for cod in the southern Gulf of St. Lawrence and 0.44 for cod on the Scotian Shelf. Availability to the surveys varied with the age of the fish. Additional uncertainty is introduced by the possibility that availability may vary as a result of changes in temperature (Baird and Bishop 1986).

The estimates of the weight of capelin in the cod stomachs can be used to estimate consumption rate at the time of sampling if gastric evacuation rate is known. Studies on the rate of evacuation of capelin from stomachs of cod at low temperature (0-6°C) are in progress.

The only major additional requirement for calculating consumption on an annual basis is seasonal information on feeding, as was collected in Div. 3L in 1985. There is, however, a major flaw with the Div. 3L study. The sampling was conducted in a specific area (Div. 3L offshore) rather than on a specific group of cod as it went through its seasonal migrations. There is a possibility that different groups of fish were sampled, depending on the season. In addition, it will be difficult to incorporate the food consumption by that part of the stock which moved inshore, since the proportion which moved inshore is not known and there was no sampling of stomachs inshore in 1985.

6.2. QUANTITY OF CAPELIN CONSUMED BY OTHER PREDATORS

Estimates of potential consumption of capelin by marine mammals (Sergeant 1973, 1976; Winters and Carscadden 1978) and seabirds (Brown and Nettleship 1984) are based on estimates of individual daily ration, population size, duration of feeding on capelin, and proportion of capelin in the diet. The estimates are based on information accumulated over a series of years. There appear to be no estimates derived from adequate sampling within a given year.

The estimates presently available show cod to be by far the major predator on capelin, although perhaps new estimates should be made. This is

particularly true for harp seals, which appear to be increasing in number and for which there has been a recent study of stomach contents (I-H. Ni, Department of Fisheries and Oceans, St. John's, Nfld. pers. comm.). A group of predators which has been ignored to date is other fish. Capelin is a major prey of American plaice on Grand Bank (Pitt 1973, unpubl. data), and is the most important prey of Greenland halibut less than 70 cm in Div. 2J,3K (Bowering and Lilly 1985). Estimates of the quantity of capelin in the stomachs of the Greenland halibut population offshore in Div. 2J,3K in autumn are similar in magnitude to the quantity estimated to be in the stomachs of the cod population (Table 4).

6.3. CAPELIN MORTALITY RATES DUE TO PREDATION

There is very little information which would permit one to estimate the mortality imposed by predators. As noted by Anderson and Lilly (1985), there has been no attempt to compare capelin production in a specific year with capelin consumption in that year by all predators, and there has been no examination of variability in annual consumption of capelin by a specific predator. The information presently available constrains one to estimates of the type provided by Brown and Nettleship (1984), who calculated that the total annual consumption of capelin by all predators east and south of Newfoundland (Div. 2J+3KLNOPs) in the 1970's (3.82 million t) was only 37% of the peak capelin biomass in 1976, but 350% of the biomass estimated for 1979. Another problem is that most studies have not considered the sizes or ages of capelin consumed by predators, so it will be difficult to apportion the mortality to individual age-groups. Even if good information on removals of capelin by predators were available, the calculation of mortality rates would be hampered by uncertainties in estimating capelin abundance. Estimates from acoustic surveys are considered to be indices of relative abundance (Carscadden 1984), and even the relative abundance of capelin younger than age 2 is poorly measured.

7. CONCLUDING REMARKS

The focus of this review has been on the predation by cod on capelin, and on the effect of this feeding relationship on the dynamics of both species. Such information is relevant primarily for long-term assessment and management. (See Beverton et al. (1984) and Shepherd (1984) for discussion of the various sorts of information relevant to short-term and long-term management.)

Although the broad patterns of the feeding by cod on capelin have been described, little is known about the dynamics of the interaction. We might wish to know if changes in capelin abundance affect cod migration patterns and cod productivity (growth, mortality and recruitment), and if changes in cod abundance affect capelin mortality and recruitment. We might also wish to answer more specific questions, such as: for each of several proposed levels of sustained fishing mortality for capelin, what is the most likely weight-at-age for cod in five years? It is hoped that current programs of sampling will provide data appropriate for addressing some of these questions.

ACKNOWLEDGEMENTS

I wish to thank colleagues who have studied various aspects of the biology of cod and capelin and have contributed much to my understanding of the interactions between the two species. In particular, I wish to acknowledge informative and stimulating discussions with S. A. Akenhead, J. R. Botta, W. H. Lear, J. C. Rice, R. Wells, and especially J. E. Carscadden.

REFERENCES

Akenhead, S. A., J. Carscadden, H. Lear, G. R. Lilly, and R. Wells. 1982. Cod-capelin interactions off northeast Newfoundland and Labrador, p. 141-148. In M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Allan, J. D. 1981. Determinants of diet of brook trout (Salvelinus fontinalis) in a mountain stream. Can. J. Fish. Aquat. Sci. 38: 184-192.

Anderson, J. T., and G. R. Lilly. 1985. Review of reported biological and technological interactions for commercial marine species of the Newfoundland Region, p.34-53. In R.Mahon [ed.] Towards the inclusion of fishery interactions in management advice. Can. Tech. Rep. Fish. Aquat. Sci. No. 1347.

Anonymous. 1981. Northwest Atlantic Fisheries Organization, Scientific Council Reports. 1981. Report of Standing Committee on Fishery Science. p. 15.

1982. Northwest Atlantic Fisheries Organization, Scientific Council Reports, 1982. Report of Standing Committee on Fishery Science. p. 34.

1986. Northwest Atlantic Fisheries Organization, Scientific Council Reports, 1986. Report of Standing Committee on Fishery Science. p. 74-77.

Baird, J. W., and C. A. Bishop. 1986. Assessment of the cod stock in NAFO Divisions 2J+3KL. NAFO SCR Doc. 86/47, Ser. No. N1163. 50 p.

Bakanev, V. S. 1981. Results of Soviet investigations on capelin in northwest Atlantic in 1980. NAFO SCR Doc. 81/10, Ser. No. N274. 10 p.

Bakanev, V. S., and K. V. Gorchinsky. 1985. Hydroacoustic survey of capelin stocks in Divisions 2J+3K and trawl survey of capelin prerecruits in Divisions 3KLNO in November 1984 - January 1985. NAFO SCR Doc. 85/52, Ser. No. N1001. 11 p.

Beverton, R. J. H., et al. 1984. Dynamics of single species - Group Report, p. 13-58. In R. M. May [ed.] Exploitation of marine communities. Springer-Verlag, New York, NY.

Bowering, W. R., and G. R. Lilly. 1985. Diet of Greenland halibut off southern Labrador and northeastern Newfoundland (Div. 2J+3K) in autumn of 1981-82, emphasizing predation on capelin. NAFO SCR Doc. 85/109, Ser. No. N1085. 16 p.

Brown, R.G.B., and D. N. Nettleship. 1984. Capelin and seabirds in the northwest Atlantic, p. 184-194. In D. N. Nettleship, G. A. Sanger and P. F. Springer [ed.] Marine birds: their feeding ecology and commercial fisheries relationships. Proc. Pacific Seabird Group Symposium, Seattle, Washington, 6-8 January 1982. Can. Wildl. Serv. Spec. Publ.

Bulatova, A. Yu. 1973. Distribution and abundance of young cod off Newfoundland in April-June, 1972. ICNAF Res. Doc. 73/22, Ser. No. 2955. 6 p.

Campbell, J. S., and G. H. Winters. 1973. Some biological characteristics of capelin, Mallotus villosus, in the Newfoundland area. ICNAF Redbook 1973(III): 137-144. (See also Addendum to ICNAF Res. Doc. 73/90, Serial No. 3048).

Carscadden, J. E. 1984. Capelin in the northwest Atlantic, p. 170-183. In D. N. Nettleship, G. A. Sanger and P. F. Springer [ed.] Marine birds: their feeding ecology and commercial fisheries relationships. Proc. Pacific Seabird Group Symposium, Seattle, Washington, 6-8 January 1982. Can. Wildl. Serv. Spec. Publ.

1986. The Southeast Shoal (Div. 3NO) capelin stock. NAFO SCR Doc. 86/53, Ser. No. N1170. 7 p.

Carscadden, J., and D. B. Atkinson. 1986. Capelin in NAFO SA2 + Div. 3K. CAFSAC Res. Doc. 86/90. 54 p.

Carscadden, J. E., and D. S. Miller. 1980. Analytical and acoustic assessments of the capelin stock in Subarea 2 and Div. 3K, 1979. NAFO SCR Doc. 80/13, Ser. No. N045. 19 p.

Chan, M., and J. Carscadden. 1976. The food and feeding of capelin (Mallotus villosus) in the Labrador area during autumn 1973. ICNAF Res. Doc. 76/20, Ser. No. 3800. 5 p.

Clark, C. W. 1985. Bioeconomic modelling and fisheries management. John Wiley & Sons, New York, NY. 281 p.

Daan, N. 1973. A quantitive analysis of the food intake of North Sea cod, Gadus morhua. Neth. J. Sea Res. 6: 479-517.

Doubleday, W. G. [ed.] 1981. Manual on groundfish surveys in the Northwest Atlantic. NAFO Sci. Coun. Studies. 2: 7-55.

Grinkevich, N. S. 1957. Year-to-year changes in the food of cod in the Barents Sea. Trudy PINRO 10: 88-105. (Can. Transl. Fish. Aquat. Sci. 223, 1959).

Gulland, J. A. 1982. Long-term potential effects from management of the fish resources of the North Atlantic. J. Cons. int. Explor. Mer. 40: 8-16.

1983. World resources of fisheries and their management, p. 839-1061. In O. Kinne [ed.] Marine ecology. A comprehensive, integrated treatise on life in oceans and coastal waters. Vol. 5, Ocean management. Part 2: Ecosystems and organic resources. John Wiley & Sons, New York.

Hansen, P. M. 1949. Studies on the biology of the cod in Greenland waters. ICES Rapp. et Proc.-Verb. 123: 1-77.

Jangaard, P. M. 1974. The capelin (Mallotus villosus). Biology, distribution, exploitation, utilization, and composition. Fish. Res. Board Can. Bull. 186. 70 p.

Jobling, M. 1982. Food and growth relationships of the cod, Gadus morhua L., with special reference to Balsfjorden, north Norway. J. Fish Biol. 21: 357-371.

Kerr, S. R. 1971. Prediction of fish growth efficiency in nature. J. Fish. Res. Board Can. 28: 809-814.

1982. Estimating the energy budgets of actively predatory fishes. Can. J. Fish. Aquat. Sci. 39: 371-379.

Kovalyov, S. M., and B. D. Kudrin. 1973. Soviet investigations on capelin in the Northwest Atlantic in 1971 and 1972. ICNAF Redbook 1973. Part III: 121-126.

Lear, W. H. 1979. Distribution, size and sexual maturity of Arctic cod (Boreogadus saida) in the northwest Atlantic during 1959-78. CAFSAC Res. Doc. 79/17. 40 p.

1984a. Discrimination of the stock complex of Atlantic cod (Gadus morhua) off southern Labrador and eastern Newfoundland, as inferred from tagging studies. J. Northw. Atl. Fish. Sci. 5: 143-159.

1984b. The winter distribution of cod in NAFO Divisions 2J, 3K, and 3L, based on research vessel catches during 1978-83. NAFO SCR Doc. 84/24, Ser. No. N799. 9 p.

1986. A further discussion of the stock complex of Atlantic cod (Gadus morhua) in NAFO Div. 2J, 3K, and 3L. NAFO SCR Doc. 86/118, Ser. No. N1245. 18 p.

Lear, W. H., and J. W. Baird. 1985. Minimum estimates of abundance of Arctic cod (Boreogadus saida) in NAFO Divisions 2J, 3K, and 3L from research vessel surveys. NAFO SCR Doc. 85/42, Ser. No. N992. 14p.

Lear, W. H., J. W. Baird, J. C. Rice, J. E. Carscadden, G. R. Lilly, and S. A. Akenhead. 1986. An examination of factors affecting catch in the

inshore cod fishery of Labrador and eastern Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 1469. 71 p.

Lilly, G. R. 1980. The food of Arctic cod, Boreogadus saida (Lepechin), off Labrador in autumn, 1978. CAFSAC Res. Doc. 80/4. 11 p.

1982. Influence of the Labrador Current on predation by cod on capelin and sand lance off eastern Newfoundland. NAFO Sci. Coun. Studies 3: 77-82.

1984a. Annual variability in the diet of Atlantic cod (Gadus morhua L.) off southern Labrador and northeast Newfoundland (Div. 2J+3K) in autumn, 1977-82. NAFO SCR Doc. 84/79, Ser. No. N868. 12 p.

1984b. Predation by Atlantic cod on shrimp and crabs off northeastern Newfoundland in autumn of 1977-82. ICES C.M.1984/G:53. 25 p.

1986. Variability in the quantity of capelin and other prey in stomachs of Atlantic cod off southern Labrador and northeastern Newfoundland (NAFO Division 2J+3K) during the autumns of 1978-85. NAFO SCR Doc. 86/80, Ser. No. N1201. 17 p.

Lilly, G. R., M. A. Almeida, and W. H. Lear. 1984. Food of Atlantic cod (Gadus morhua) from southern Labrador and eastern Newfoundland (Div.2J, 3K, and 3L) in winter. NAFO SCR Doc. 84/88, Ser. No. N878. 9 p.

Lilly, G. R., and J. R. Botta. 1984. Food of Atlantic cod (Gadus morhua L.) near Bonavista, Newfoundland in 1983. NAFO SCR Doc. 84/51, Ser. No. N838. 8 p.

Lilly, G. R., and J. Carscadden. 1986. Capelin in Division 3L and their occurrence in the NAFO regulatory area. NAFO SCR Doc. 86/84, Ser. No. N1206. 15 p.

Lilly, G. R., and A. M. Fleming. 1981. Size relationships in predation by Atlantic cod, Gadus morhua, on capelin, Mallotus villosus, and sand lance, Ammodytes dubius, in the Newfoundland area. NAFO Sci. Coun. Studies 1: 41-45.

Lilly, G. R., and S. Meron. 1986. Propeller clam (Cyrtodaria siliqua) from stomachs of Atlantic cod (Gadus morhua) on the southern Grand Bank (NAFO Div. 3NO): natural prey or an instance of net feeding? ICES C.M. 1986/G:36. 13 p.

Lilly, G. R., and D. R. Osborne. 1984. Predation by Atlantic cod (Gadus morhua) on short-finned squid (Illex illecebrosus) off eastern Newfoundland and in the northeastern Gulf of St.Lawrence. NAFO SCR Doc. 84/108, Ser. No. N905. 16 p.

Lilly, G. R., and J. C. Rice. 1983. Food of Atlantic cod (Gadus morhua) on the northern Grand Bank in spring. NAFO SCR Doc. 83/87, Ser. No. N753. 35 p.

Lilly, G. R., R. Wells, and J. Carscadden. 1981. Estimates of the possible consumption of capelin by the cod stocks in Divisions 2J+3KL and 3NO. NAFO SCR Doc. 81/8, Ser. No. N272. 9 p.

Macdonald, J. S., K. G. Waiwood, and R. H. Green. 1982. Rates of digestion of different prey in Atlantic cod (Gadus morhua), ocean pout (Macrozoarces americanus), winter flounder (Pseudopleuronectes americanus), and American plaice (Hippoglossoides platessoides). Can. J. Fish. Aquat. Sci. 39: 651-659.

Majkowski, J., and W. S. Hearn. 1984. Comparison of three methods for estimating the food intake of a fish. Can. J. Fish. Aquat. Sci. 41: 212-215.

Majkowski, J., and K. G. Waiwood. 1981. A procedure for evaluating the food biomass consumed by a fish population. Can. J. Fish. Aquat. Sci. 38: 1199-1208.

Martin, O. R. 1956. Spanish Research Report, 1955. ICNAF Ann. Proc. 6: 55-57.

Martin, O. R., and R. L. Costa. 1954. Report on the cruise carried out by the Spanish vessel "Vendaval" in the waters off Newfoundland February-April 1953. ICNAF Ann. Proc. 4: 49-54.

Martin, O. R., and A. R. Lucio. 1955. Report on the cruise by the Spanish trawler "Mistral" in the waters off Newfoundland, June-July, 1954. ICNAF Ann. Proc. 5: 51-57.

Maxim, C. 1980. Capelin (Mallotus villosus) catch, effort, and biological characteristics in the Romanian fishery in Division 2J, September-October 1979. NAFO SCR Doc. 80/4, Ser. No. N030. 10 p.

Miller, D. S. 1979. An acoustic estimate of juvenile Arctic cod (Boreogadus saida) abundance in ICNAF Divisions 2J and 3K 1978. CAFSAC Res. Doc. 79/12. 11 p.

1986. Estimates of capelin (Mallotus villosus) biomass from hydroacoustic surveys in Divisions 3LNO in 1985 and 1986. NAFO SCR Doc. 86/79, Ser. No. N1200. 11 p.

Miller, D. S., and J. E. Carscadden. 1981. Acoustic survey results for capelin (Mallotus villosus) in Divisions 2J3K and 3LNO, 1980. NAFO SCR Doc. 81/5, Ser. No. N269. 10 p.

Miller, D. S., B. S. Nakashima, and J. E. Carscadden. 1982. Capelin acoustic surveys in NAFO Divisions 2J+3K, 3LNO, and 3L, 1981-82. NAFO SCR Doc. 82/54, Ser. No. N547. 12 p.

Minet, J. P., and J. B. Perodou. 1978. Predation of cod, Gadus morhua, on capelin, Mallotus villosus, off eastern Newfoundland and in the Gulf of St. Lawrence. ICNAF Res. Bull. 13: 11-20.

Nakashima, B. S., J. E. Carscadden, and G. R. Lilly. 1982. Capelin (Mallotus villosus) biology and history of the fishery in the northern Gulf of St. Lawrence, Div. 4RS. CAFSAC Res. Doc. 82/29. 32 p.

Palsson, O. K. 1983. The feeding habits of demersal fish species in Icelandic waters. Rit Fiskideildar. 7: 1-45.

Pinhorn, A. T. [ed.]. 1976. Living marine resources of Newfoundland-Labrador: status and potential. Bull. Fish. Res. Board Can. 194. 64 p.

Pitt, T. K. 1973. Food of American plaice (Hippoglossoides platessoides) from the Grand Bank, Newfoundland. J. Fish. Res. Board Can. 30: 1261-1273.

Popova, O. A. 1962. Some data on the feeding of cod in the Newfoundland area of the Northwest Atlantic, p. 228-248. In Y. Y. Marti [ed.] Soviet Fisheries Investigations in the Northwest Atlantic, VNIRO-PINRO, Moskva. (Transl. from Russian for U.S. Dep. Int. Nat. Sci. Found., Washington, D.C., by Israel Prog. Sci. Transl. 1963.)

Powles, P. M. 1958. Studies of the reproduction and feeding of Atlantic cod (Gadus callarias L.) in the southwestern Gulf of St. Lawrence. J. Fish. Res. Bd. Can. 15: 1383-1402.

Rae, B. B. 1967. The food of cod in the North Sea and on west of Scotland grounds. Mar. Res., 1967 (1): 1-68.

Seliverstov, A. S., and L. I. Serebrov. 1979. Status of capelin stocks in Divisions 2J and 3K in 1978. ICNAF Res. Doc. 79/30, Ser. No. 5356. 12 p.

Sergeant, D. E. 1973. Feeding, growth, and productivity of northwest Atlantic harp seals (Pagophilus groenlandicus). J. Fish. Res. Board Can. 30: 17-29.

1976. The relationships between harp seals and fish populations. ICNAF Res. Doc. 76/125, Ser. No. 4011. 5 p.

Shepherd, J. G. 1984. The availability and information content of fisheries data, p. 95-109. In R. M. May [ed.]. Exploitation of marine communities. Springer-Verlag, New York, NY.

Sinclair, M., J. J. Maguire, P. Koeller, and J. S. Scott. 1984. Trophic dynamic models in light of current resource inventory data and stock assessment results. Rapp. P.-v. Reun. Cons. int. Explor. Mer. 183: 269-284.

Smith, S. J., and G. D. Somerton. 1981. STRAP: A user-oriented computer analysis system for groundfish research trawl survey data. Can. Tech. Rep. Fish. Aquat. Sci. 1030: iv + 66 p.

Stanek, E. 1973. Observations on food and feeding of cod (Gadus morhua L.) in Labrador, Newfoundland and Nova Scotia waters. Prace. Mor. Inst. Ryb. 17: 7-26. (Transl. from Polish by Fish. Mar. Serv. Transl. Ser. 3171, 1974).

1975. The percentage of capelin in the stomach contents of cod in ICNAF Subareas 2 and 3. ICNAF Res. Doc., No. 75/5, Ser. No. 3433. 9 p.

Templeman, W. 1965. Some instances of cod and haddock behaviour and concentrations in the Newfoundland and Labrador areas in relation to food. ICNAF Spec. Publ., No. 6: 449-461.

1966. Marine resources of Newfoundland. Bull. Fish. Res. Bd. Can. 154: 1-170.

Templeman, W., and A. W. May. 1965. Research vessel catches of cod in the Hamilton Inlet Bank area in relation to depth and temperature. ICNAF Spec. Publ. 6: 149-165.

Thompson, H. 1943. A biological and economic study of cod (Gadus callarias L.) in the Newfoundland area including Labrador. Nfld. Dept. Nat. Resour. Fish. Bull. 14: 1-160.

Turuk, T. N. 1968. Seasonal changes of cod feeding in the Labrador and Newfoundland areas in 1964-66. Trudy-PINRO, 23: 370-382. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. 1937,1971).

1978. The feeding of Labrador and Newfoundland cod on capelin. Trudy PINRO 41: 67-73. (Transl. from Russian by Can. Transl. Fish. Aquat. Sci. 4580, 1979).

Waiwood, K., and J. Majkowski. 1984. Food consumption and diet composition of cod, Gadus morhua, inhabiting the southwestern Gulf of St. Lawrence. Environ. Biol. Fish. 11: 63-78.

Wankowski, J.W.J. 1979. Morphological limitations, prey size selectivity, and growth response of juvenile Atlantic salmon, Salmo salar. J. Fish Biol. 14: 89-100.

Wankowksi, J.W.J., and J. E. Thorpe. 1979. The role of food particle size in the growth of juvenile Atlantic salmon (Salmo salar L.). J. Fish Biol., 14: 351-370.

Wells, R. 1980. Age and growth of Arctic cod (Boreogadus saida) taken off Labrador in September, 1978. CAFSAC Res. Doc. 80/5. 4 p.

Winters, G. H. 1983. Analysis of the biological and demographic parameters of the northern sand lance, Ammodytes dubius, from the Newfoundland Grand Bank. Can. J. Fish. Aquat. Sci. 40: 409-419.

Winters, G. H., and J. E. Carscadden. 1978. Review of capelin ecology and estimation of surplus yield from predator dynamics. ICNAF Res. Bull. 13: 21-30.

Table 1. The food of Atlantic cod off southern Labrador and northeastern Newfoundland (NAFO Division 2J, 3K) in the autumns of 1982 and 1985 (from Lilly 1986).

	Percent Occurrence		Percent by weight[a]		Mean PFI[a,b]	
	1982	1985	1982	1985	1982	1985
Invertebrata (misc.)	7.02	14.44	0.56	0.87	0.01	0.02
Anthozoa	4.94	0.33	1.01	0.11	0.01	+
Ctenophora	5.07	2.22	1.16	0.20	0.01	+
Gastropoda	4.49	2.63	0.31	0.17	+	+
Cephalopoda	3.74	3.98	0.44	0.58	0.01	0.01
Polychaeta	28.75	14.85	0.86	0.41	0.03	0.02
Ophiuroidea	2.15	0.16	0.06	+	+	+
Crustacea (total)	87.54	89.99	23.20	23.42	0.37	0.64
Hyperiidae	29.14	63.11	1.73	12.14	0.04	0.35
Gammaridea	43.25	31.43	0.79	0.44	0.04	0.02
Mysidacea	22.83	23.27	0.15	0.23	0.01	0.02
Euphausiacea	10.57	12.88	0.18	0.33	0.01	0.02
Natantia						
Pandalus borealis	24.39	18.14	4.80	2.95	0.08	0.07
Pandalus montagui	3.41	5.42	0.54	0.84	0.01	0.02
Others and unid.	40.46	36.52	3.93	3.55	0.07	0.10
Reptantia						
Chionoecetes opilio	15.28	5.29	8.34	2.17	0.08	0.03
Hyas coarctatus	3.15	0.82	1.44	0.14	0.01	+
Others and unid.	8.88	5.13	0.92	0.49	0.01	0.01
Others and unid.	11.25	6.11	0.40	0.15	0.01	0.01
Pisces (total)	50.70	62.74	66.65	71.81	0.74	1.80
Mallotus villosus	9.85	26.59	15.95	36.17	0.28	0.95
Boreogadus saida	0.68	5.83	0.25	5.47	+	0.15
Gadidae (unid.)	0.39	1.03	1.45	1.21	0.01	0.02
Zoarcidae	1.27	0.66	5.74	0.35	0.03	+
Sebastes sp.	2.80	0.41	2.15	3.42	0.02	0.03
Pleuronectidae	2.60	2.59	16.24	1.79	0.08	0.02
Others	2.73	4.19	3.91	2.36	0.02	0.03
Unid.	40.36	51.09	20.98	21.05	0.30	0.59
Unidentified and misc.	54.99	23.64	5.77	2.41	0.09	0.06
Total					1.27	2.55
No. of stomachs	3075	2437				
Percent empty	2.6	0.8				

[a] + indicates presence but <0.005.

[b] Mean partial fullness index $PFI = \frac{1}{n} \sum \frac{W_i}{L_i^3} \times 10^4$ where W_i is the weight of indicated prey type in fish i, L_i is the length of fish i, and n is the number of fish examined.

Table 2. The food of Atlantic cod on the northern Grand Bank (NAFO Division 3L), May - June, 1979 (from Lilly and Rice 1983).

	Percent[a] occurrence	Percent by weight	Mean PFI[b]
Mollusca		1.4	0.03
Misc. Invertebrates and Unidentified		2.4	0.07
Crustacea			
Amphipoda		3.0	0.11
Euphausiacea		9.1	0.27
Natantia		2.4	0.08
Reptantia		27.0	0.52
Other and Unidentified		0.3	0.01
Pisces			
Mallotus villosus	19.1	15.0	0.43
Ammodytes sp.	19.8	28.0	0.74
Miscellaneous		9.1	0.11
Unidentified		2.3	0.06
Total		100.0	2.43
No. of Stomachs: 1898			
Percent empty: 2.4			

[a]Provided only for those taxa not initially identified at a lower taxonomic level.

[b]See Table 1 for definition of PFI.

Table 3. Quantities of capelin in stomachs of the Atlantic cod population in NAFO Division 2J, 3K at the time of sampling in autumn 1982 (from Lilly 1986).

Length group (cm)	Number of stomachs	Capelin in stomachs		Cod abundance (X 10^{-3})	Total capelin in stomachs (t)
		PFI[a]	av. wt.(g)		
Div. 2J					
9-17	11	0.00	0.00	466	0.0
18-26	77	0.06	0.09	2,077	0.2
27-35	168	0.61	2.03	9,249	18.8
36-44	308	0.64	4.03	26,786	108.0
43-53	216	0.33	3.84	12,143	46.6
54-62	310	0.25	5.28	30,783	162.5
63-71	284	0.30	9.12	26,908	245.4
72-80	188	0.22	9.53	6,456	61.5
81-89	83	0.20	12.05	1,433	17.3
90-98	41	0.25	23.00	632	14.5
>98	21	0.00	0.48	355	0.2
Total	1,707			117,288	675.0
Div. 3K					
9-17					
18-26	43	0.07	0.12	1,165	0.1
27-35	160	0.02	0.06	3,214	0.2
36-44	130	0.16	0.92	3,898	3.6
45-53	239	0.21	2.45	11,912	29.2
54-62	253	0.16	2.89	17,145	49.5
63-71	245	0.21	6.90	16,319	112.6
72-80	187	0.12	4.90	5,509	27.0
81-89	81	0.36	20.33	1,544	31.4
90-98	25	0.68	53.45	677	36.2
>98	5	0.00	0.00	408	0.0
Total	1,368			61,791	265.5

[a]See Table 1 for definition of PFI.

Table 4. Quantities of capelin (tons) estimated to be present in stomachs of predator populations in Division 2J, 3K at the time of sampling in autumn, 1981-83.

Predator	Division	1981	1982	1983
Cod[a]	2J	2209	675	1215
	3K	269	266	420
	Total	2478	941	1635
Greenland halibut[b]	2J	1016	1098	
	3K	261	275	
	Total	1277	1373	
Grand Total		3755	2314	

[a]Estimated as in Table 3.

[b]From Bowering and Lilly 1985.

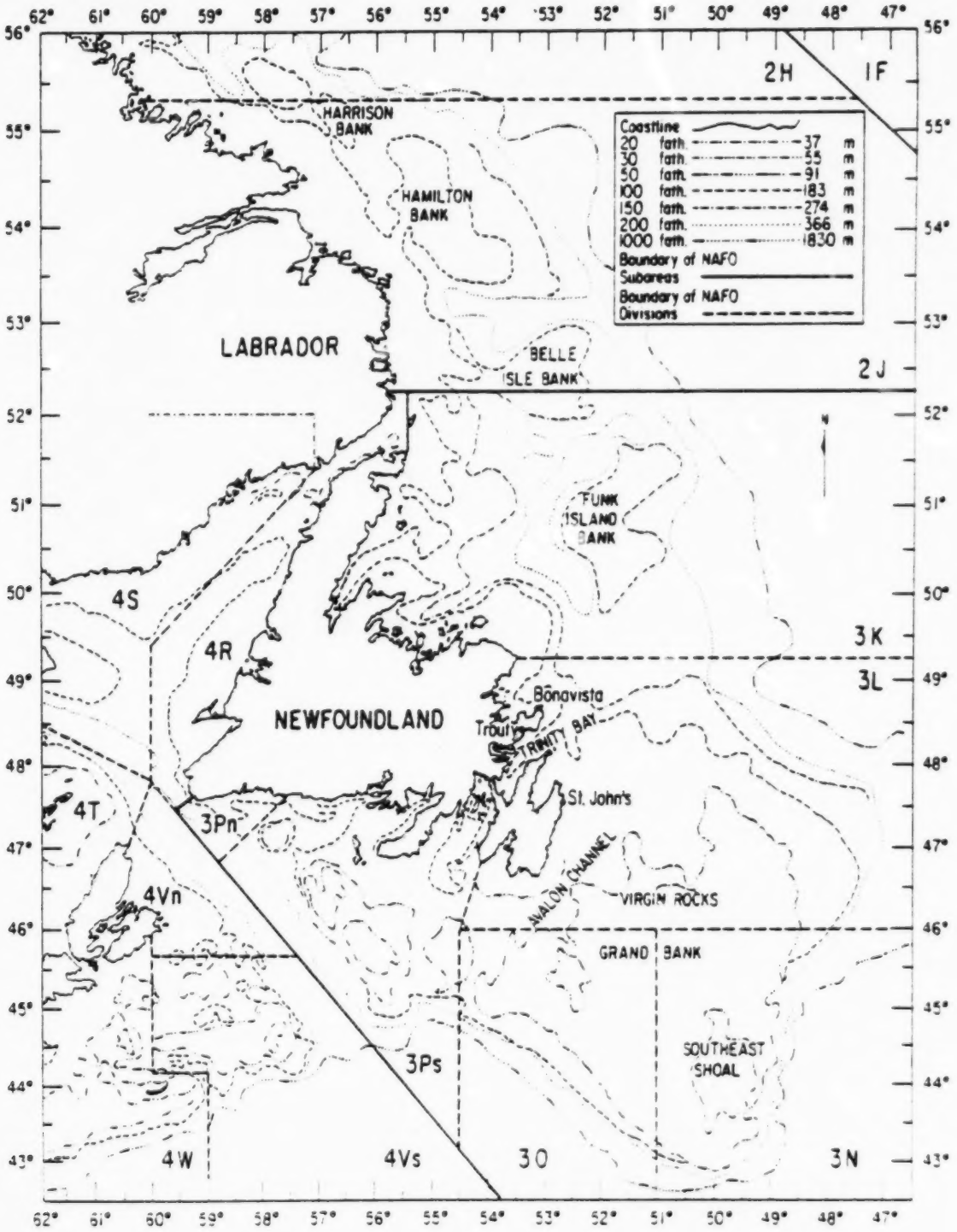

Fig. 1. Map of Newfoundland and Labrador, showing NAFO Divisions and localities mentioned in the text.

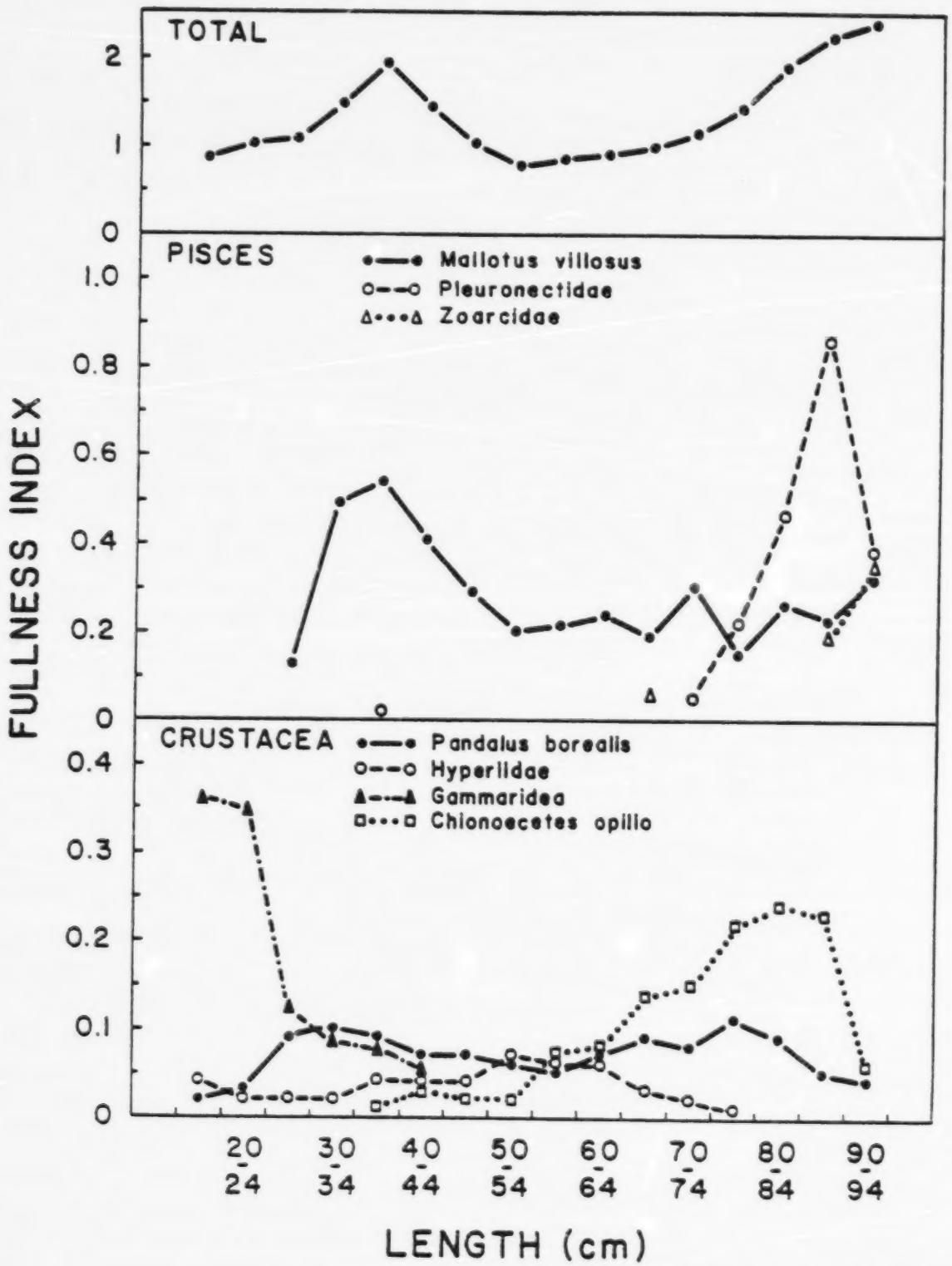

Fig. 2. Changes in total fullness index, and partial fullness indices for major prey, with increasing cod length: Div. 2J3K, autumn 1982 (from Lilly 1984a)

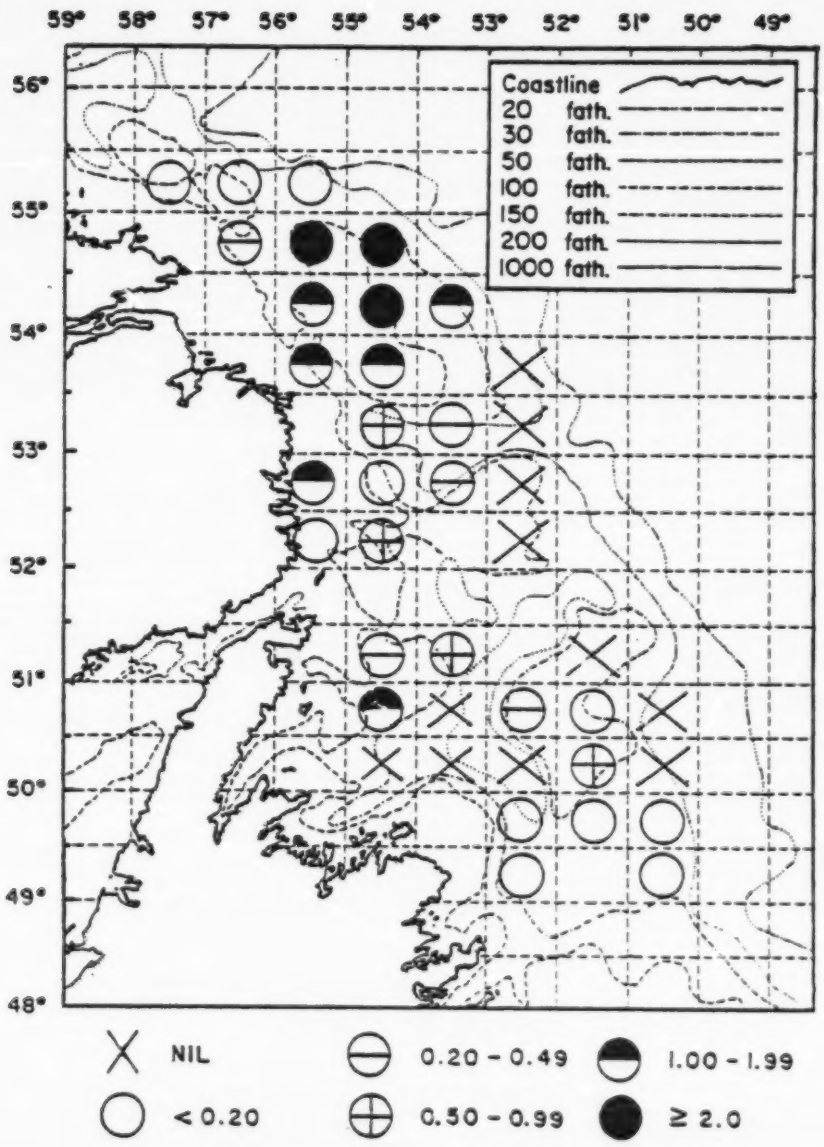

Fig. 3. Geographic variation in mean partial fullness index for capelin from cod stomachs in 1981. All stomachs collected from cod (30-69 cm) caught in each 0.5° latitude x 1.0° longitude area were combined. Data from areas with fewer than 5 stomachs were not plotted. Many samples from between approximately 51°00'N and 52°30'N were lost (from Lilly 1984a).

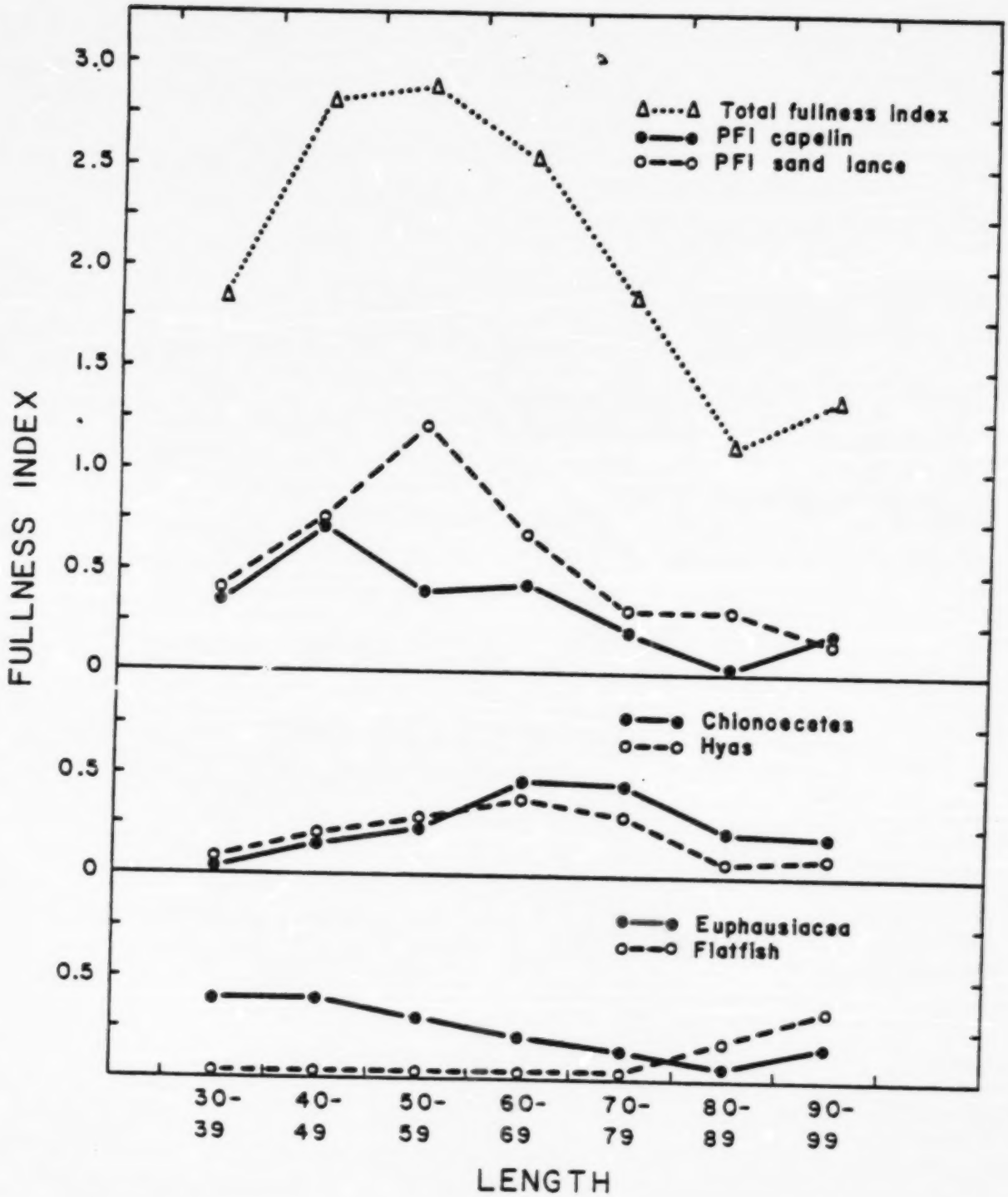

Fig. 4. Changes in total fullness index, and partial fullness indices for major prey, with increasing cod length: Div. 3L, May-June 1979 (from Lilly and Rice 1983).

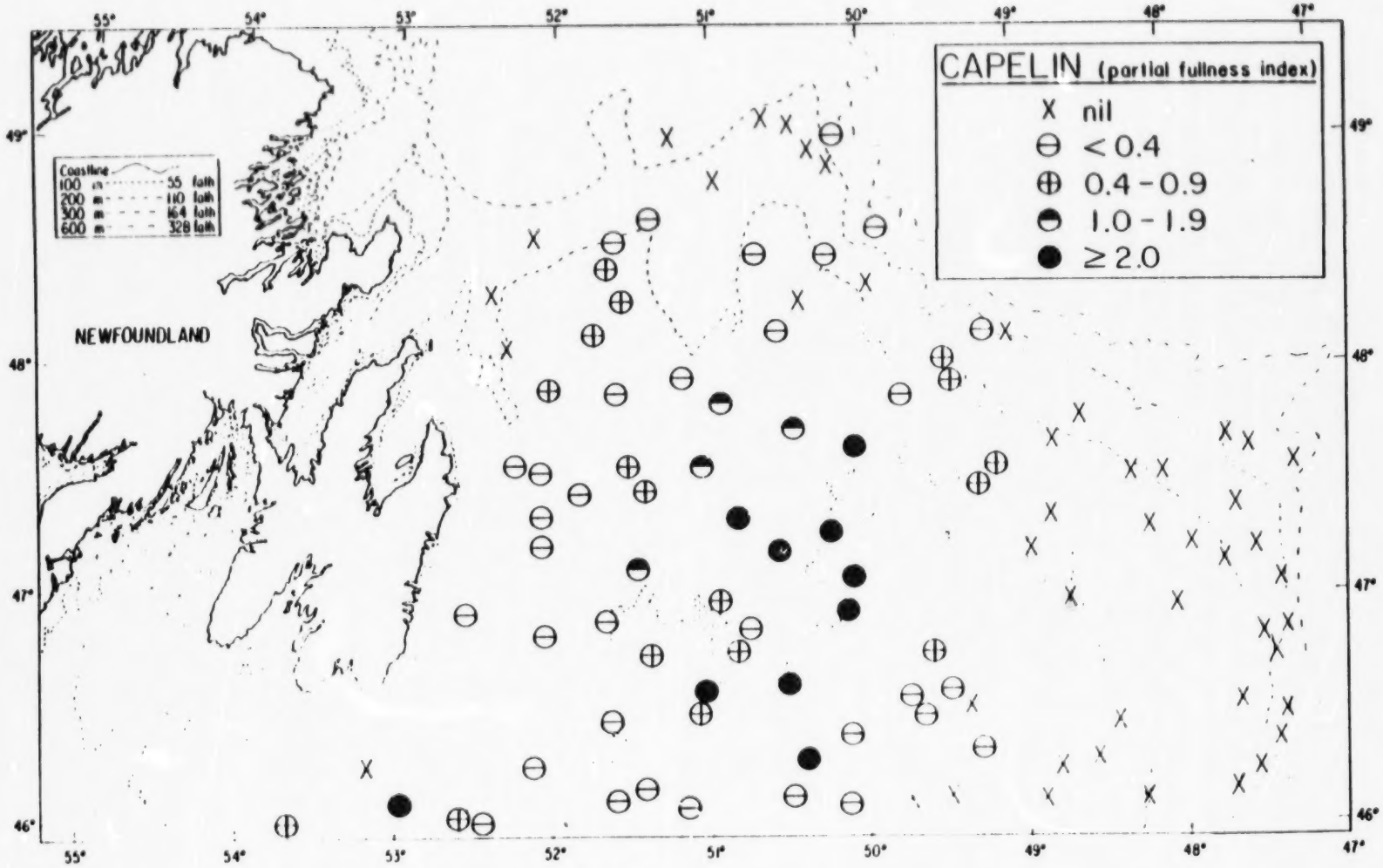

Fig. 5. Partial fullness indices of capelin from cod stomachs by fishing set: Div. 3L, May-June 1979 (from Lilly and Rice 1983).

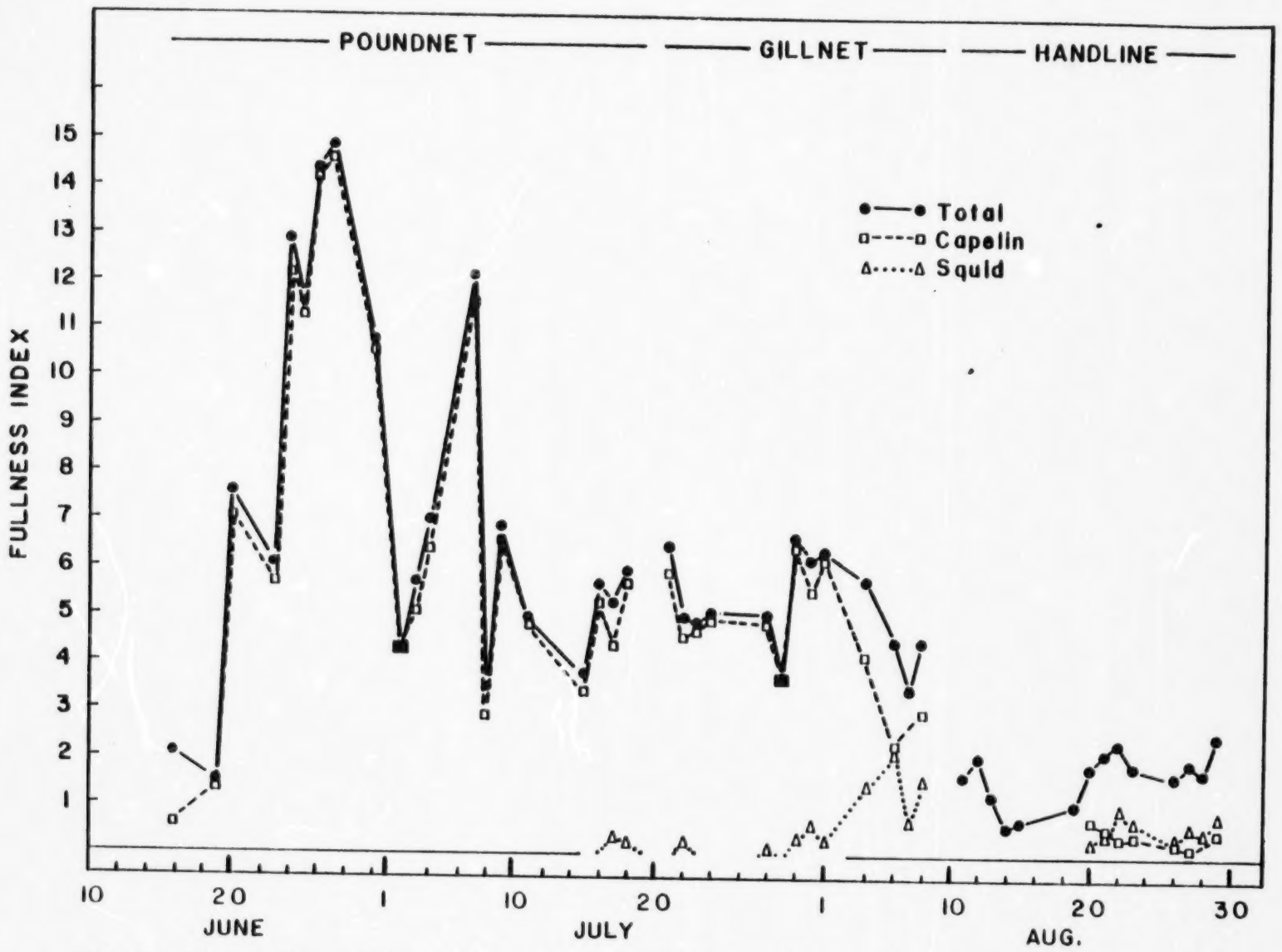

Fig. 6. Total fullness index, and partial fullness indices for capelin and squid, in samples of cod collected from the commercial inshore fishery at Trouty, Trinity Bay, during summer 1980 (from Lilly and Osborne 1984).

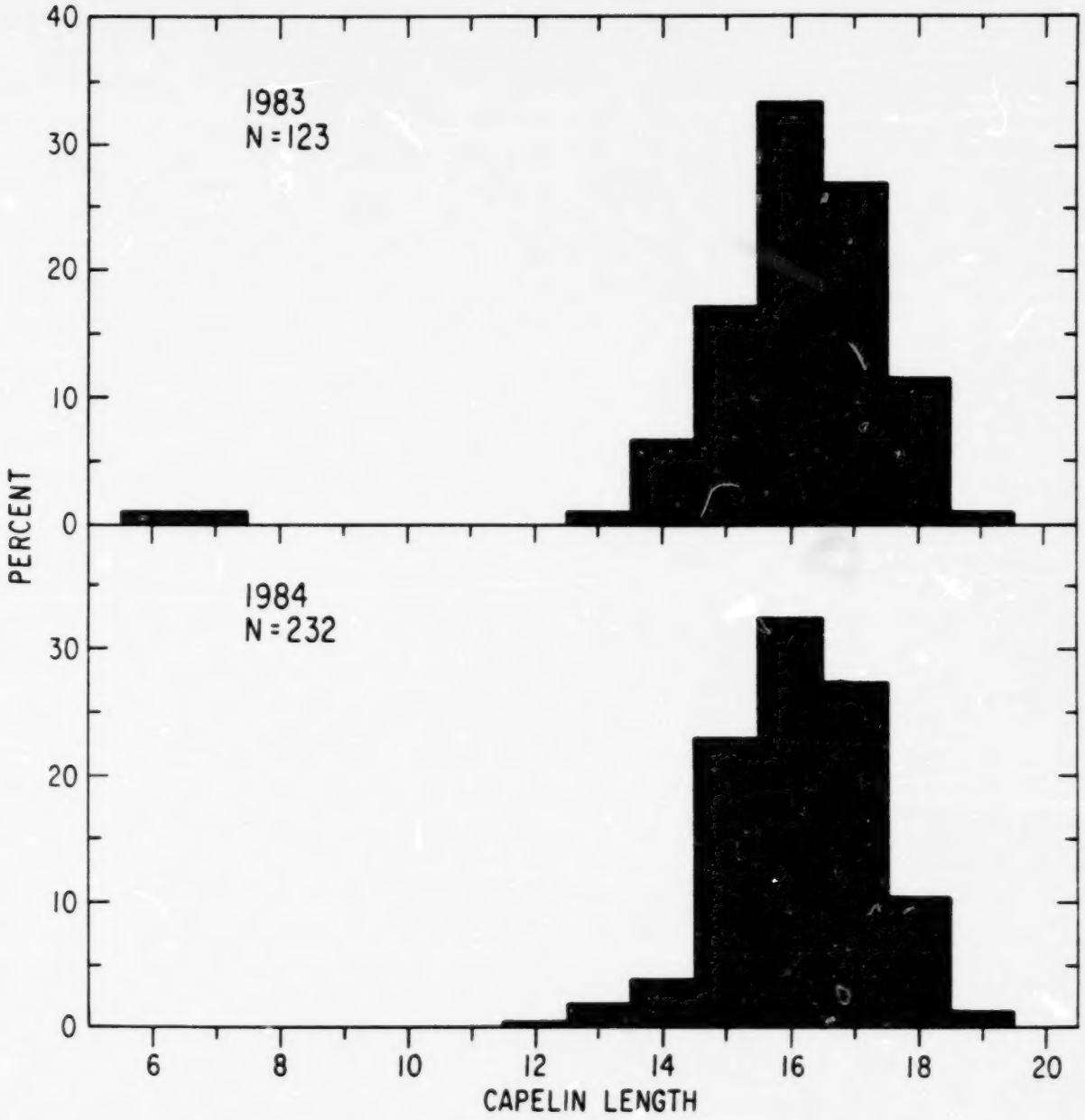

Fig. 7. Length frequency of capelin from stomachs of cod caught in traps at Bonavista, 1983 and 1984.

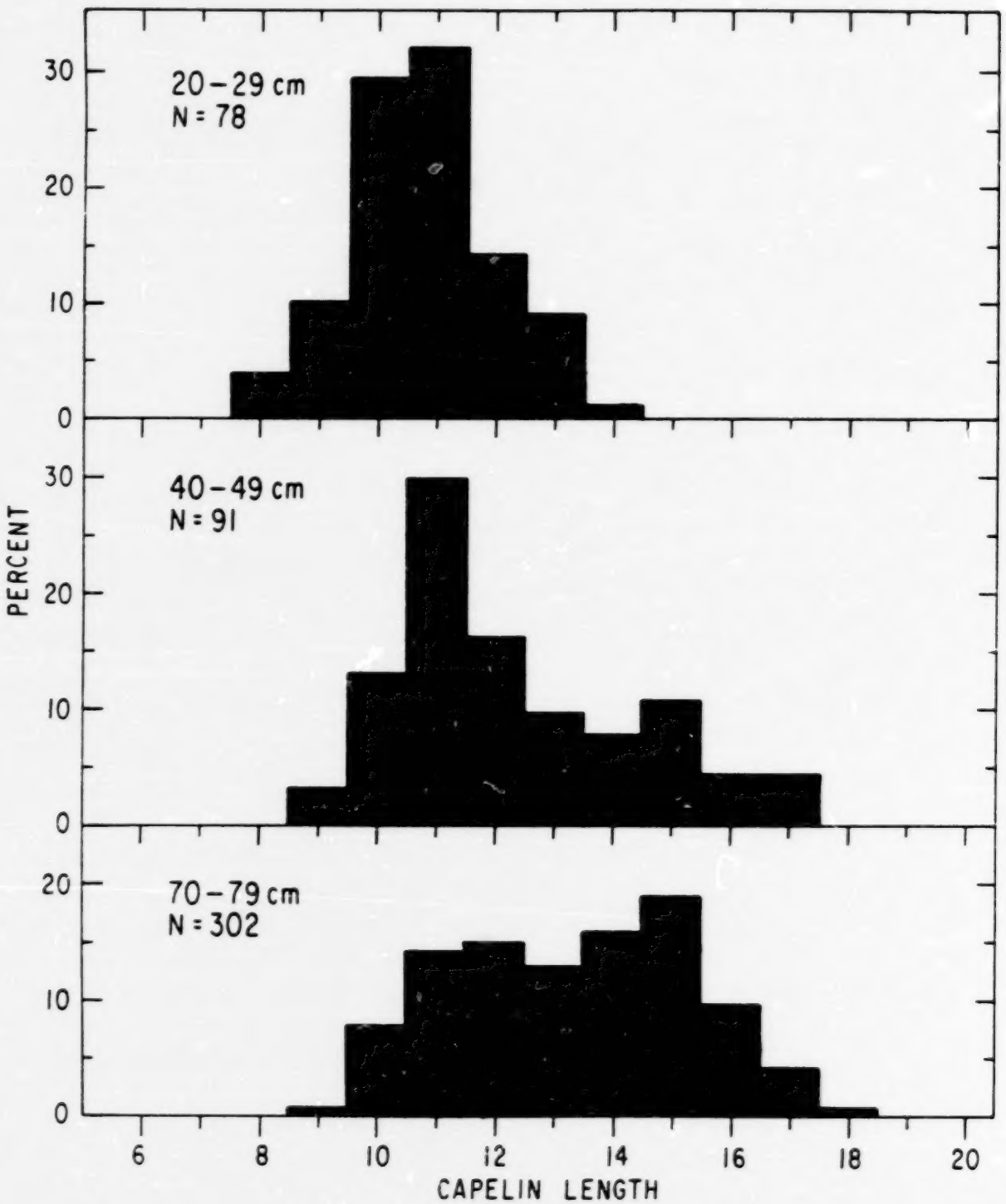

Fig. 8. Length frequency of capelin from stomachs of cod (10 cm length-groups) caught by bottom otter-trawl (Gadus Atlantica trip 49) in northwestern Div. 3L, April 1981.

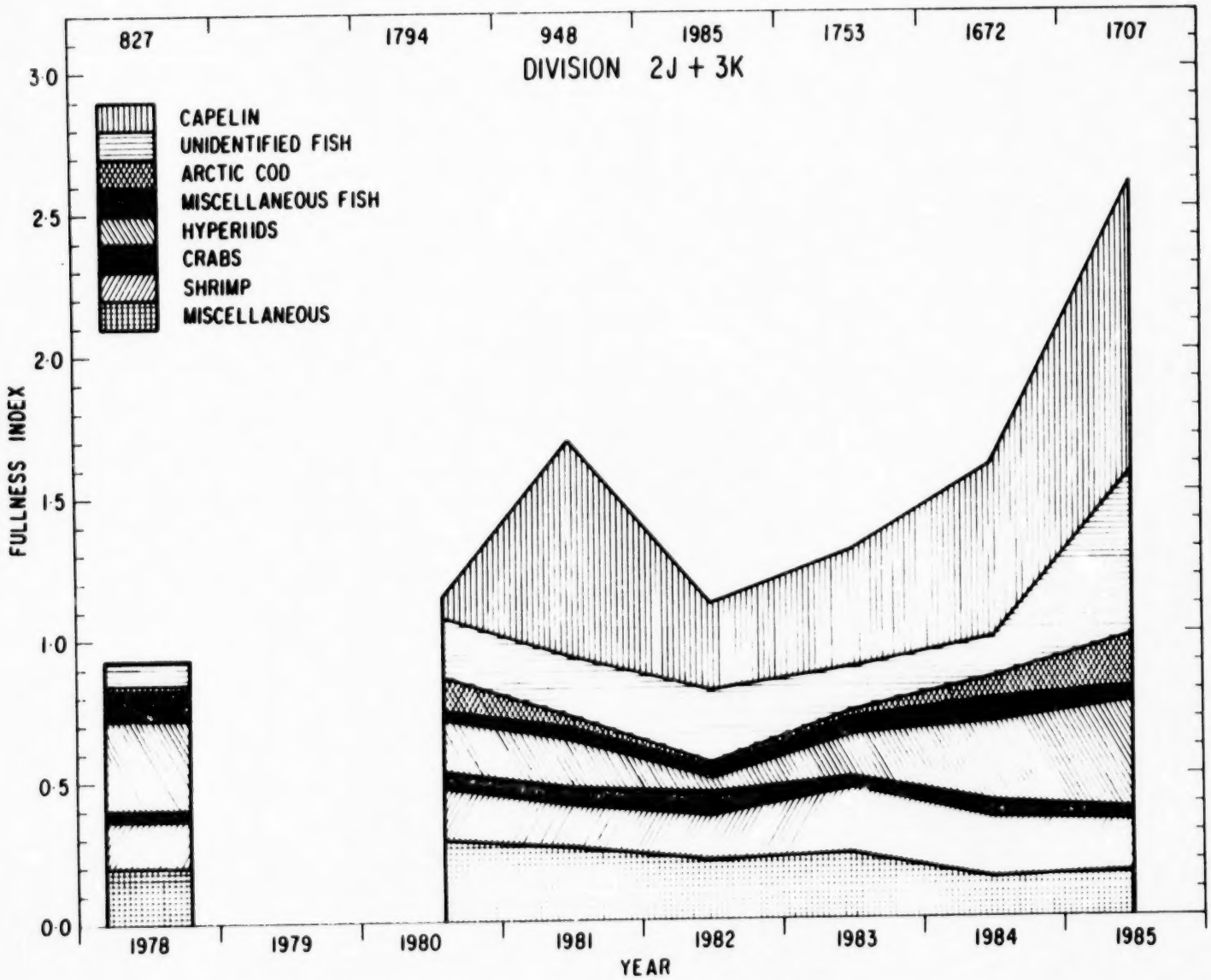

Fig. 9. The prey composition (expressed as fullness index) of Atlantic cod (36-71 cm only) in NAFO Div. 2J+3K in the autumns of 1978 and 1980-85. Arctic cod includes Gadidae. The number of stomachs examined each year is given at the top (from Lilly 1986).